EVOLUTION, HEREDITY AND VARIATION

D. WARD CUTLER

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TO

MY FATHER AND MOTHER

EVOLUTION HEREDITY AND VARIATION

By

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PREFACE TO NEW EDITION

SINCE its original publication much detailed investigation has been carried out on the fundamental facts of biology outlined in this book. The inclusion of this recent research would considerably increase the size of the volume, but would in no way alter the general principles which are discussed. I have, therefore, decided to maintain the text unchanged except for a few corrections and the substitution of a new diagram in place of the one on page 77. The genetical implications of the theory of natural selection have been ably discussed by R. A. Fisher in his recent book, *The Genetical Theory of Natural Selection*, and should be consulted by those readers who wish to pursue further study of this fundamental part of biology.

D. W. C.

HARPENDEN, 1932.

PREFACE

THE purpose of this little book is to present, in as simple a manner as possible, some of the results of modern research on the great questions of evolution, variation and heredity.

These subjects have often been dealt with before, but either only one of the three problems has been treated, or else the amount of material included has been so great as to render the book too bulky for the average reader.

Moreover, during the past few years breeding experiments have yielded results of such importance to the understanding of some of the fundamental principles of biology that an attempt to put them into simple form, and to show what new light they throw upon the question of evolution and variation, is of interest.

It should be stated at the outset, however, that though the facts given are beyond dispute, yet some of the conclusions expressed in the last chapter, and those regarding the inheritance of acquired characters, would not be accepted by some eminent biologists of to-day. But such disagreement in the interpretation of facts is inevitable in experimental science; and is valuable, since it stimulates further research.

Now that the teaching of biology is becoming more and more common in secondary schools it is hoped that this book will be useful to members of the higher forms who are being taught the elementary anatomy and physiology of plants and animals.

But I should like to feel that it was regarded less as a school book proper than as a short introduction to the study of the great problems which lie at the base, not only of biology, but also of sociology.

I am grateful to my wife and my father for reading through the manuscript and giving advice, from the standpoint of non-scientific people, on the arrangement of the matter ; and to Miss L. M. Crump for preparing figures three and four, reading the manuscript and greatly assisting me in preparing the index and correcting the proofs. Especially are my thanks due to Mrs. Hodson for much valuable criticism and advice.

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I

EVOLUTION : GEOGRAPHICAL AND GEOLOGICAL EVIDENCE

Early theories of the origin of species—Theory of organic evolution—Evolution and geographical distribution —Evolution of the horse.

AS far back as history reaches the question as to how living creatures have arisen has been pondered over by thinking people. The problem of the creation is of continued interest and can ever be relied upon to promote discussion and speculation. It can easily be understood that views concerning this great question were in early times exceedingly numerous, for there were few definitely established facts on which to base discussion, and therefore little possibility of putting any theory to the rigid test of scientific examination.

Theory of Special Creation—This theory, widely held until the teaching of Charles Darwin captivated men's minds, is an exceedingly old one, and is in fact the literal interpretation of the story of creation as set forth in the first chapter of Genesis. It is indeed far older than the Genesis documents, and scholars now regard it as coming down from the earliest Mesopotamian civilizations. Acceptance of it, of course, implied that "in the beginning" all animals and plants were created and had remained unchanged ever since. Such was the official teaching of the Church until the middle of the nineteenth century, and though by certain naturalists, such as Linnæus, slightly altered to fit the facts discovered by the advance of knowledge, it was in essentials that held by the early Christian Fathers, though an honourable exception must be given to St. Augustine, who would have taught otherwise.

The theory was fated, however, to suffer a severe shock from the discoveries of animals and plants preserved as fossils in the rocks. These fossils were evidently the remains of an older population, and the puzzle was how to account for them. The suggestion of Phillip Gosse that they were purposely placed in the rocks by the Creator to rebuke man's curiosity, though ingenious, was not satisfying; and it was left for the great naturalist Cuvier to formulate the theory of catastrophism.

Theory of Catastrophism.—Cuvier (1769–1832) suggested that the world had been the scene of a series of vast local cataclysms by which the plants and animals were exterminated, but in certain cases preserved in the rocks. After each catastrophe the region was repopulated, not by a new act of creation, but by the migration of animals and plants from surrounding areas which had not suffered.

The theory was soon expanded by other men far beyond its original scope, and there was postulated a re-creation after each catastrophe.

In 1848 Alcide D'Orbigny wrote: "The first creation shows itself in the Silurian stage. After its annihilation through some geological cause or other, a second creation took place a considerable time after in the Devonian stage, and, twenty-seven times in succession, distinct creations have come to re-people the whole earth with its plants and animals after each of the geological disturbances which destroyed everything in living nature. Such is the fact, certain but incomprehensible, which we confine ourselves to stating without endeavouring to solve the superhuman mystery which envelops it."

Theory of Organic Evolution.—The foregoing views all assumed that the various species of animals and plants were fixed and unchangeable. With the advent of the theory of organic evolution the doctrine is entirely changed. The animals and plants of to-day are the direct descendants of animals and plants of yesterday which have become modified to their changing surroundings.

Evolution must be regarded as a change from the relatively simple to the complex; highly specialized animals, such as the mammals, are the visible results of the evolutionary process acting on less specialized animals such as the prehistoric reptiles.

Evidence of Evolution.—Many different theories of organic evolution have appeared, and during the past few years a great deal of discussion has centred upon the truth of one or other of them. Such discussions have been by no means confined to the journals of scientific societies, but have crept into the pages of the popular press, with the result that some people have been led to think that evolution itself was being questioned, whereas in reality the criticism is directed against some particular theory as to the way in which evolution has proceeded.

That evolution has taken place in the past and is still going on is beyond dispute. In this chapter, therefore, some of the principal reasons for holding this view are given.

Geographical Evidence.—Perhaps the best way to illustrate this line of evidence is to take as an example the one which impressed Darwin so much. During his memorable voyage in the *Beagle* (1831–1836) the Galapagos, a chain of islands some 600 miles west of South America, were visited. With characteristic enthusiasm he at once began collecting as many of the animals and plants as could be obtained, and on classifying them found to his surprise that each of the islands had its own characteristic animal population; but—which was even more surprising—the species on one island, though distinctive, were yet similar to those on another; and the general population of all the islands resembled that of the adjoining mainland. How to account for this was extremely puzzling except on the assumption that the species on the islands and on the mainland were blood relations claiming their descent from a common ancestor. Thus Darwin's attention was drawn to the question of the origin of species.

It is probable that at an earlier period in the earth's history these islands were joined together to form one large land mass, which was itself once connected with the West Indies and Central America.

There was then presumably a much smaller number of species than to-day, and they were distributed over the entire region. After separation from the American continent the species became isolated through the gradual breaking up of this land mass into smaller islands. Subsequently these solitary groups of animals became differentiated into the several forms now characteristic of the various islands, showing descent from a common ancestor with eventual specialization.

Australia affords another example. There was a time in the past ages when the only mammals[1] on the earth were the Marsupials, or pouched animals, and at this period Australia, originally connected with the Asiatic continent, became separated from it by the sea. This ocean barrier sufficed to prevent in later times the migration into Australia, from other parts of the world, of the higher species of mammals which had been evolved. This explains the curious fact that to-day Australia is the home of many Marsupials, but of none of the higher mammals, except bats, to which the sea is no barrier ; a dog, whose presence is not yet explained, and rabbits, which are known to have been introduced by man.

Geological Evidence.—Many people are familiar with the objects known as fossils without knowing exactly their significance. Organic remains, whether of plants or bodies of animals, may be naturally preserved under certain conditions by becoming impregnated with

[1] "*Mammals*" are those animals in which the new individual undergoes all the early and developmental stages of growth (termed *embryo, foetus*) in a special cavity of the female parent, the *uterus*, or *womb*. The necessary exchange of material involved in growth taking place through a series of membranes (*placenta*), shed at birth, which make contact with the maternal blood vessels. Full development of form is already attained at birth, but feeding is at first from milk formed in certain glands of the skin (*mammary glands*) of the mothers. In "*marsupials*" this whole process is found in an incomplete stage, and the young at birth are lodged in an external pouch, or fold, of skin covering the mammary glands.

mineral substances in solution, which in due course harden and dry, giving an exact reproduction in stone. So complete are some of these petrifactions that sections may be cut for microscopic examination, showing the minutest details of structure. The most favourable conditions are those obtaining under water—lake and ocean floors, where silt continually falls to make mud or ooze, in which the form remains complete and crushed ; e.g. our chalk downs were thus formed.

It is evident that we have, therefore, in the very shell of our planet the history of its transformations, to be traced by observing the superposition of one stony layer, or stratum, upon another, wherever boring or mining operations, or the natural overturning of volcanic action make such study possible. A list of the main divisions, or "geological periods" as they have been called, is given for reference. (Fig. 1). One of the strongest proofs of evolution is given by the study of fossils, for in a large number of cases it is now possible to trace an almost perfect series of forms, leading from a relatively simply organized creature to the specialized type now living. Palæontologists (those who study fossil animals) are continually adding links to the chain of descent of various animals, and one can say with Huxley, "if zoologists and embryologists had not put forward the theory of evolution, it would have been necessary for palæontologists to invent it."

Evolution of the Horse.—Perhaps one of the best and most familiar series is that dealing with the genealogy of the horse. The working out of the main lines of descent of this animal has engaged the attention of many men of science. But especial interest has been taken in it by H. F. Osborn, and by the staff of the

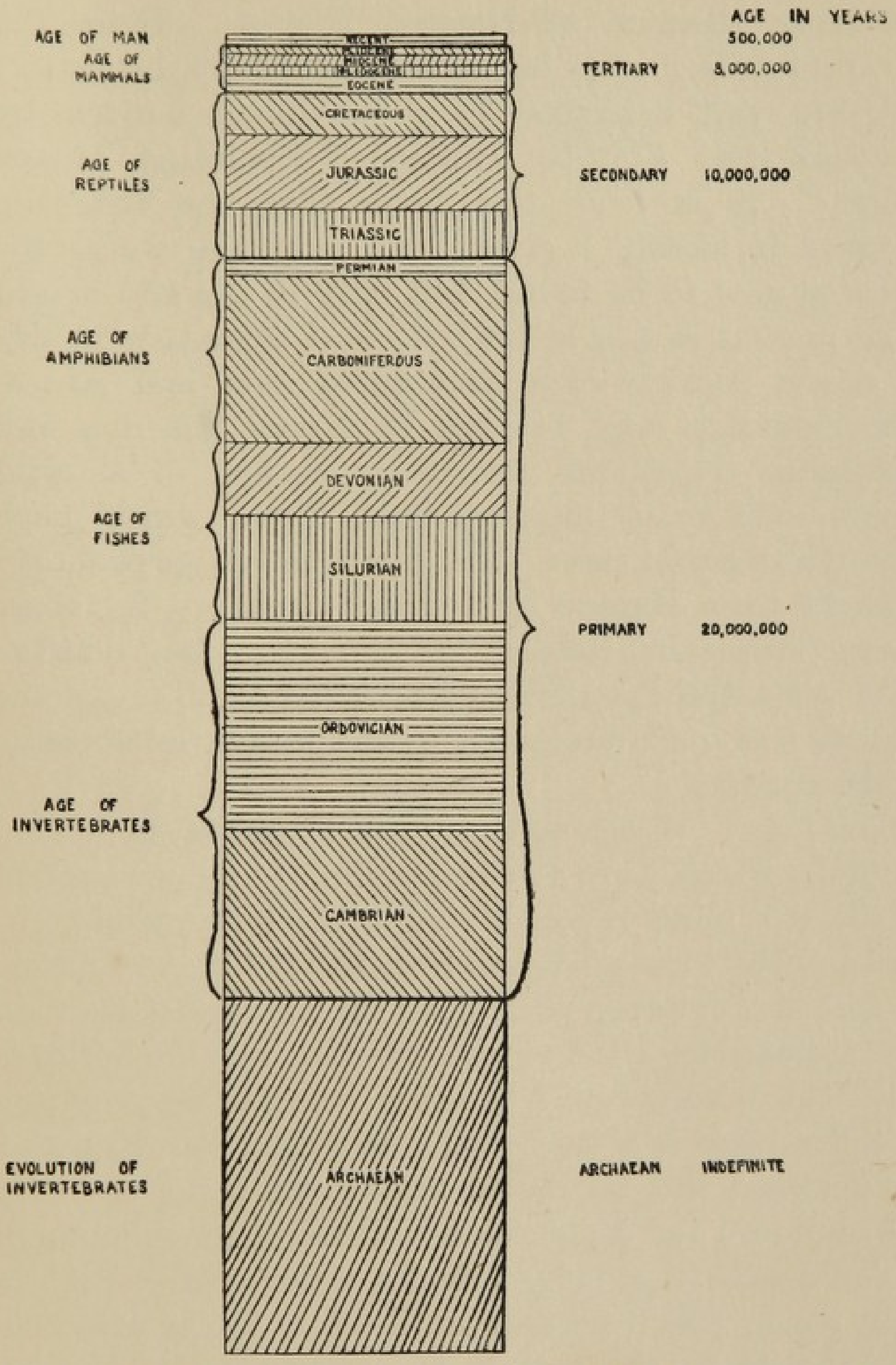


Fig. 1.—General Scheme of the stratified rocks; giving on the right the evolutionary succession of animals, and on the left the age of the formations. It must be remembered that the ages given are only approximate.

American Museum of Natural History. There the various fossils of early horses are beautifully displayed; and are well described in a handbook written by Matthew and Chubbe, entitled "Evolution of the Horse." It is from this book that the following account is largely derived. All over the world the horse is now to be found, but only in the Old World is he present as a wild animal, and there only in dry or desert regions such as Central Asia and Africa. The mustangs and broncos of North America and Australia, sometimes incorrectly spoken of as wild horses, are really domesticated forms which have lapsed into a wild state. These creatures were probably brought from Europe by the early settlers, for there is no evidence that horses lived in the New World at the time when the Spaniards first visited there; and the animal was quite unknown to the Indian inhabitants of the country.

The horse belongs to the group *Ungulata*, or hoofed animals, which have the thigh and the upper part of of the arm more or less buried in the body, whilst the heel and the wrist are raised from the ground in walking so that the creature goes along on the tips of its toes. The animals are fitted to terrestrial life and are herbivorous, the omnivorous pig being a notable exception. A collar bone is not present; it would be of no use, the forward and backward movement being the only one required for progression. Turning for a moment to the dentition, there is found a well-developed set of milk teeth, which persists until adult age is attained. The molars in the permanent set are massive, with broad crowns, which have deep folds of enamel, well adapted for the process of grinding the vegetable food material (Fig. 4). Important as all these distinctive features are, they are not so apparent as the characteristic which divides the horse from all other animals, namely, the fact that it has but one toe on each foot, which is known to be the third or middle digit The hoof on which the animal stands, and which supports the weight of the body, is a modified nail, corresponding to that of man or to the claw of the dog or cat. Besides the main bone of the leg there are two slender little bones, one on each side, called the splint bones. These are the remains of the second and fourth bones to which the second and fourth digits of other animals are attached.

The teeth of the horse are characteristic. The molars are shaped like a prism and their grinding surfaces exhibit a complicated pattern of ridges and valleys. In the fossil horses the crowns, as we shall see later, were short, with a deep constriction between the crown and the roots, called the neck. The valleys were shallow and there was no trace of the cement deposit to be found later on, the whole exposed surface being enamel. Then as evolution proceeded the ridges became more worn, and the dentine was exposed, thus forming islands round the enamel. With the progress of time the crowns of the teeth elongated, the valleys deepened and the ridges became more elongated; in order to give support to these ridges and valleys the cavities became filled with cement, and as the crown wore down an admirable grinding surface was formed composed of patches of dentine and cement, separated by hard enamel.

But other peculiarities are to be noted in the horse. The two long bones of the fore arm, the ulna and the radius, separated in many animals, are consolidated into one bone, and the same consolidation is seen in the bones of the lower leg, the tibia and the fibula. The lengthening of the foot and the stepping on the toe raises the heel of the horse much above the ground ; it forms the hock joint, bending backwards as the knee bends forwards. In this as in various other ways, the legs are especially fitted for swift running over hard level ground, just as the teeth are suited for grinding the wiry grasses which grow on the open plain.

Origin and Early Ancestry.—The origin of all horse-like animals is probably from an extinct stock of creatures known as the *Condylarthra*, of which *Phenacodus*, once described as a "five-toed horse," is an example. Its structure is that of a primitive animal. In build *Phenacodus* was slender, with straight limbs, each possessing five toes. The body was, however, chiefly supported on three, the median one being somewhat enlarged, well hoofed and extending beyond the others. The bones of the arm and leg were quite distinct one from another, and the fusing and lengthening of the wrist and ankle bones, characteristic of the modern horse, had not commenced. In size the animal was about four and a half feet long and three feet high.

The evolution of the horse through the Tertiary period, or the age of mammals, is an excellent example of the theory of evolution by means of natural selection, and of the manner in which series of animals become suited to their environment. The ancestry of the horse family has been traced back almost to the beginning of the Tertiary epoch without a single break of importance. During the period (Fig 2), probably nearly three million years in duration, all the parts of the bodies of these animals experienced great changes, especially in the teeth and feet, becoming adapted more and more perfectly to their particular environ

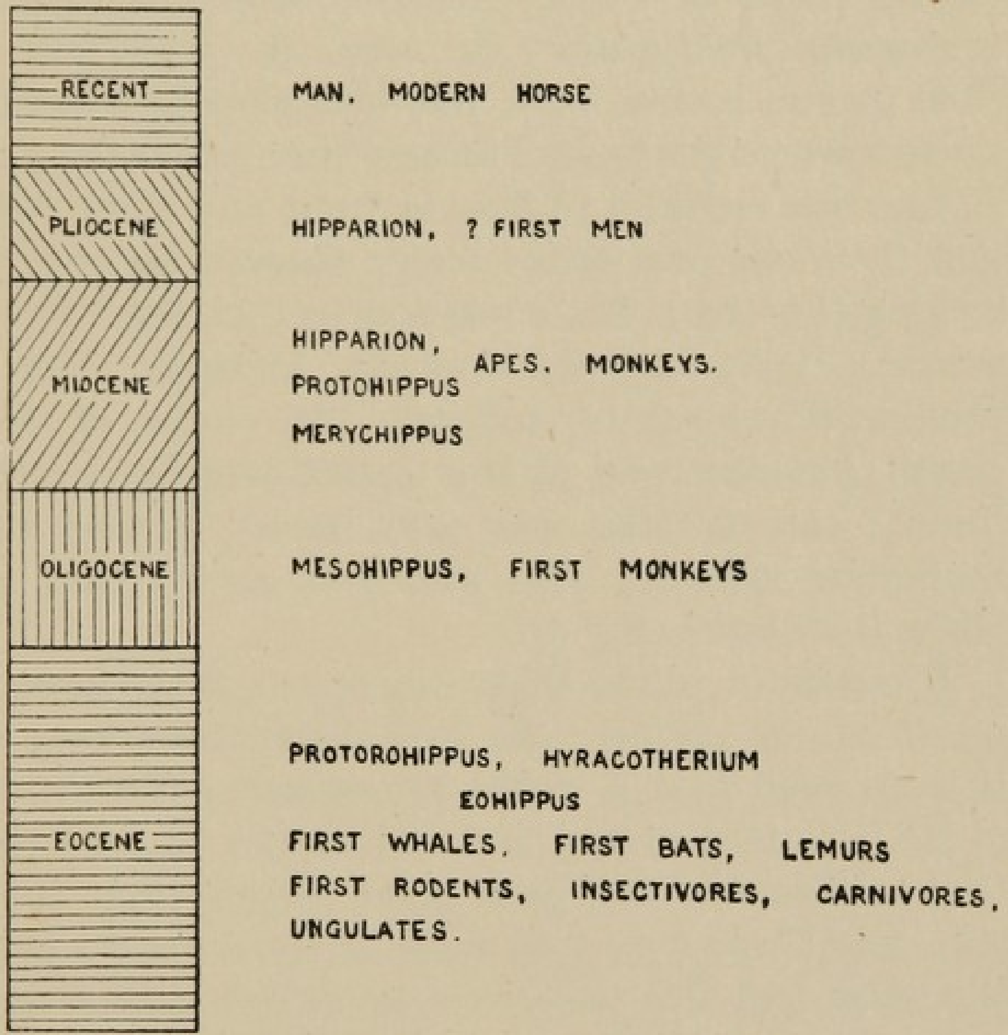


FIG. 2.—General Scheme of the Tertiary rocks.

ment, the plains of a great plateau region with scanty herbage.

It is interesting to remark that in the early ancestors there was so little suggesting a horse that, when the remains of one of them was first found, the animal was named by the great palæontologist, Richard Owen, the *Hyracotherium* or Coney Beast. The relationship of this creature to the horse was not recognized until several of the intermediate stages between it and its modern descendants were brought to light.

The first recognizable ancestor of the horse was found in the rocks of North America and was named by geologists *Eohippus*. In size it was not more than eleven inches high, but had already advanced a stage towards the horse-like condition, since the number of toes was reduced to four in front and three behind; and the wrist and ankle bones showed signs of interlocking (Fig. 3). There was also in this, the "Eocene" period, *Protorohippus*, showing, however, but little further development towards the horse of to-day. North America was at this period largely covered by forest; the climate was very moist, giving rise to numerous streams with meadows and grassy plains along the banks (Fig 4).

Mesohippus, of the Oligocene epoch, is the next landmark in our review. At this stage there were three toes on each foot, a splint representing the fifth digit of the fore foot of the animals of the Eocene period. The middle toe was now much larger than the side toes, and these bore very little of the animal's weight; the teeth had also become more complex (Fig. 4).

During this period the climate had become arid, producing woodlands, meadows and dry prairie; this had caused the disappearance of many lines of evolution though from others the horses of the next (Miocene) period originated. One of these, *Protohippus*, was distinctly horse-like. In regard to teeth it was at the stage described on p. 19. It was about thirty-six inches in height at the shoulder. The feet had but one toe touching the ground. The side toes were complete

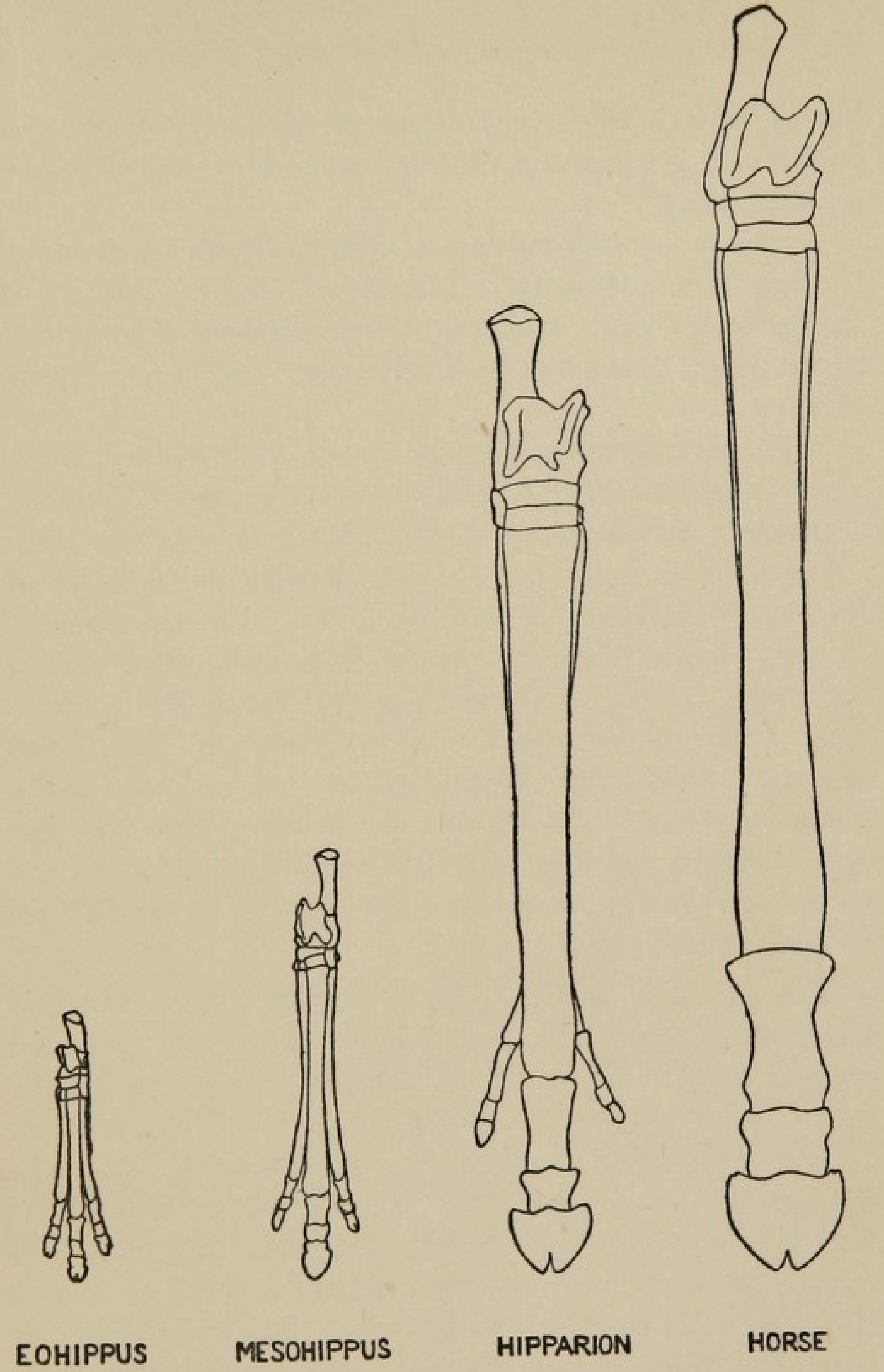


Fig. 3.—Hind feet (drawn to scale) of the horse and some of its ancestors, showing the gradual disappearance of all toes except the third one.

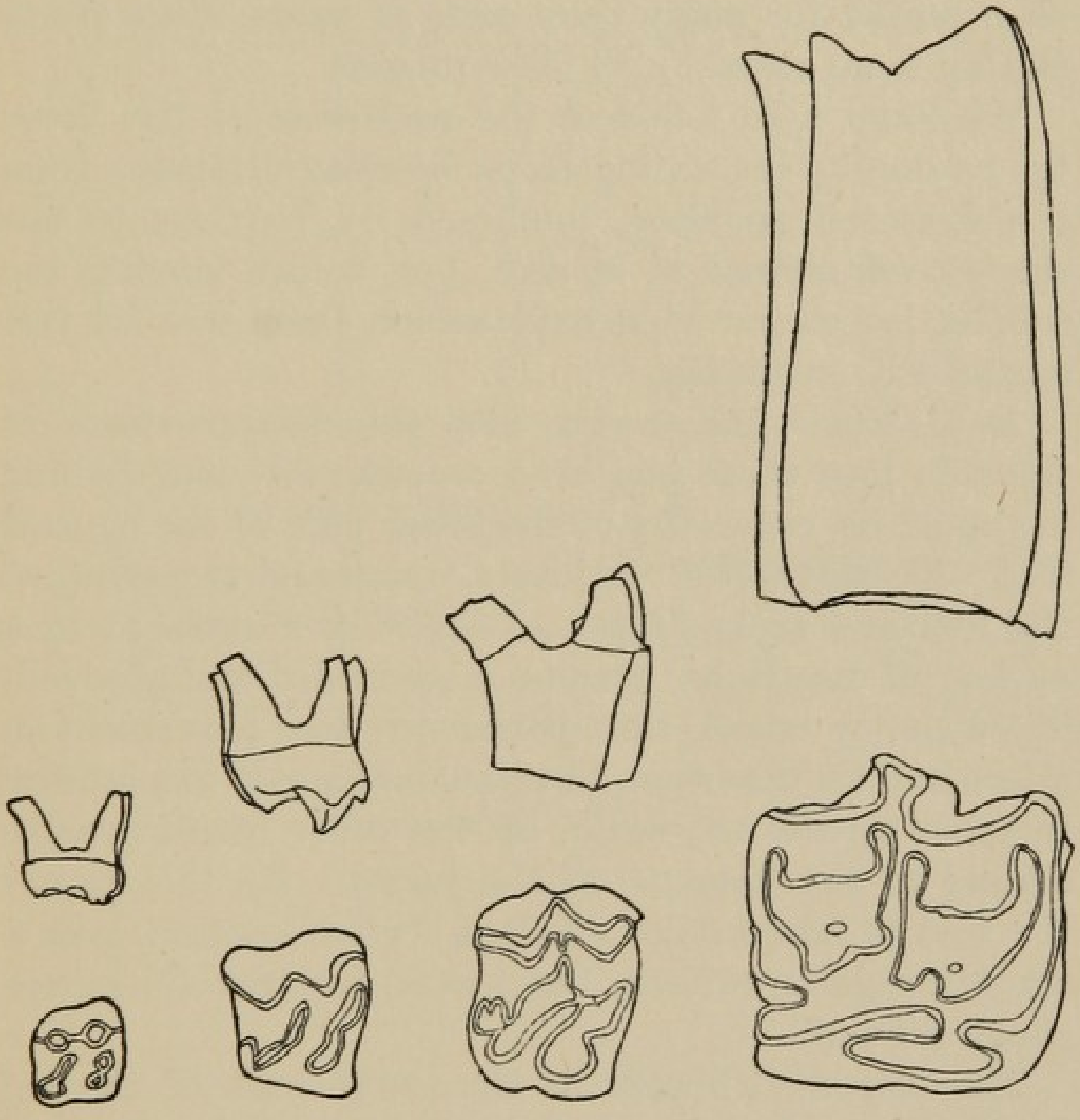
but smaller in size, in fact never touched the ground and were apparently useless, an indication of their passing away.

A closely related genus was *Merychippus*, interesting because it is certainly in the direct line of descent of the modern horse ; and from it were derived the various types which flourished in the Miocene and then became extinct.

In the next great geological epoch, the Pliocene, there was a wide distribution of the genus *Hipparion*, marking a distinct advance upon the creatures already considered. The teeth are almost identical with those of the horse and are abundantly coated with cement. The arm bones (ulna and radius) have undergone almost complete fusion, and the ulna appears as a ridge. The same modification has occurred in the bones of the hind leg, complete fusion having taken place between the tibia and the fibula. The toes are still three in number, but the second and fourth are so reduced in size that they are only to be considered as rudiments.

The Modern Horse.—And now we have reached the period when the horse as we know it appeared on the earth. In the Pleistocene epoch we no longer meet with horse-like animals, but with modern horses with their single digit on each foot, the rudiments of the second and fourth being the splint bones previously mentioned, and with the ulna and radius fused throughout their whole length, as is also the case with the tibia and fibula. The crowns of the teeth are much larger, the skull and, indeed, the whole of the animal has increased in size (Figs. 3, 4).

The epoch with which we are now dealing is called the Age of Man, or the Quaternary period, and is the last and by far the shortest of the great divisions of geological time.



EOHIPPUS MESOHIPPUS PARAHIPPUS HORSE

Fig. 4.—Teeth (drawn to scale) of the Horse and some of its ancestors. The lower row shows the crowns with the gradual increase in complication of folding to form a grinding surface ; the upper row is a side view showing the increase in the length of the root.

In the early part of the Quaternary period species of wild horses were to be found on every continent except Australia. Remains of these true native horses occur in Brazil, Ecuador, and in all parts of the United States. In America all the remains are in a petrified condition, which means that they must have been buried for many thousands of years, since petrifaction is an exceedingly slow process.

We have now followed the evolution of the horse by gradually increasing steps of specialization, from the five-toed ancestor, predicted by Huxley, to the single-toed animal of to-day, but before leaving the subject let us see what explanation there was for this remarkable evolution.

As Matthew has shown, with the disappearance of the side toes there has been considerable lengthening of the limbs, especially of the lower part of the leg and foot. The surfaces of the joints, which at first resembled the ball and socket type, so enabling movement in a variety of directions, became more keeled and grooved, like a pulley wheel, thus permitting free movement in a fore and aft direction, but limiting largely the motion in other directions, while, on the other hand, greatly adding to the strength of the joints. By this means the foot is made more efficient for locomotion over a smooth regular surface, but less so for travelling over rough ground.

The increased length in the lower part of the leg increases the length of the stride, and swiftness is attained, but a much greater strain is put upon the ankle and toe joints. This is compensated by the change from the ball and socket joint to the pulley joint. The consolidation of the two bones in the lower part of the legs (ulna and radius in the fore legs, tibia and fibula in the hind legs) gave additional stability, at the expense of flexibility.

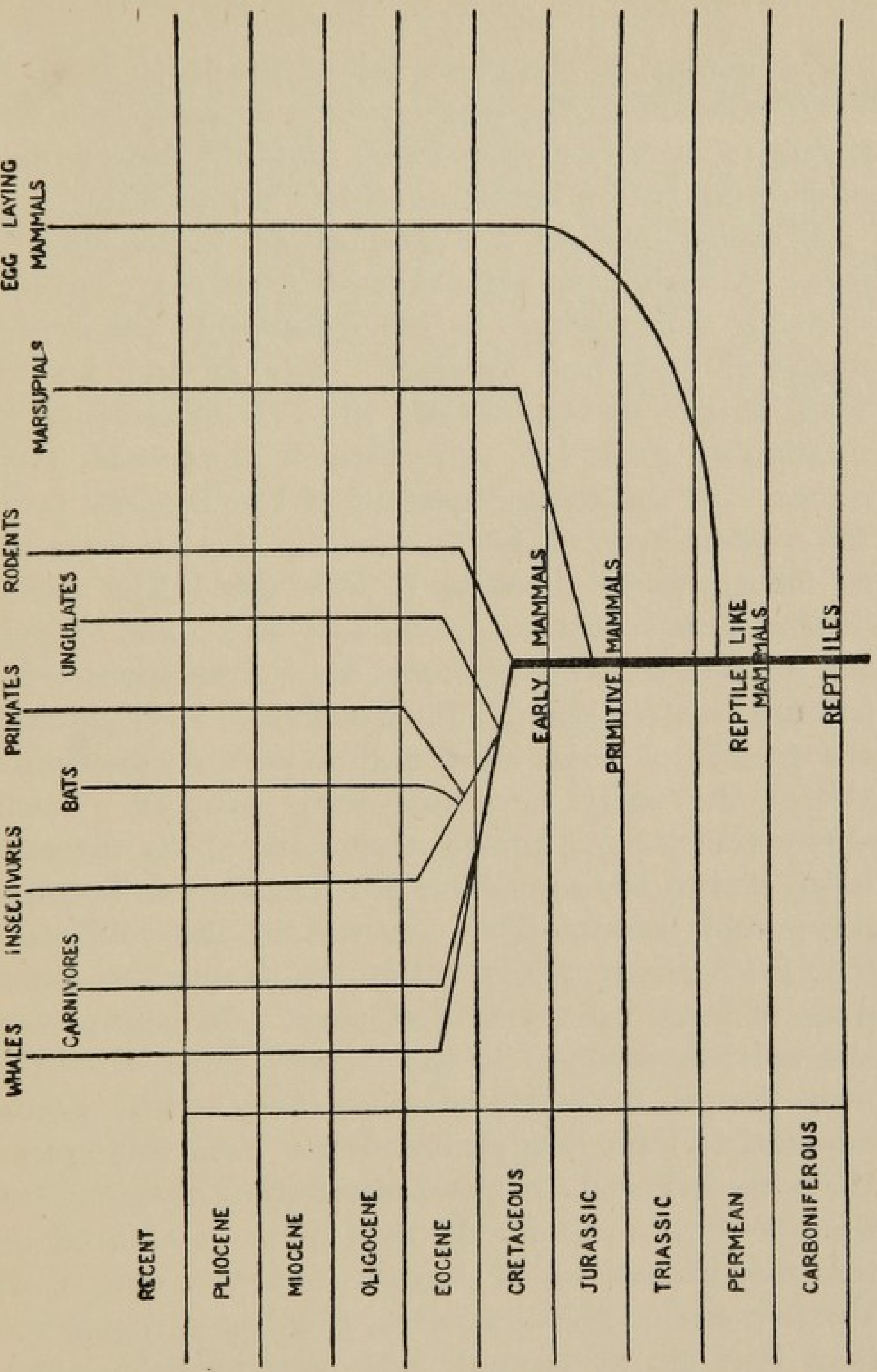


Fig. 5.—Diagram showing the origin of the mammals from reptiles in the Carboniferous period, and the subsequent differentiation of the modern orders of mammals.

The change in the character of the teeth from the short-crowned to the long-crowned enables the animal to subsist on wiry grasses which require a large amount of chewing before becoming of any use as food.

All these changes are adaptations to the environment in which the animal lived; as the conditions varied so the creatures became adapted to the requirements of their new habitats. The modern horse is fitted to live on dry plains, and this adaptation was in parallel evolution with that of the plains themselves. At the commencement of the Tertiary period the western part of North America was by no means so far above sea level as it is to-day. The climate at that time was in all probability moist and tropical, for remains of tropical forest trees even extended as far north as Greenland. Such a climate would promote the growth of forest trees, and to such a condition of things the early mammals were adapted. During this period the continents were rising above the ocean level, and at the same time the climate was becoming dryer and colder. This advance of the cold would thin the forest to a large extent and favour the appearance of large open tracts of plain. In consequence, the animals adapted to the tropical forest conditions were forced to migrate unless they could become adapted to their new surroundings. The ancestors of the horse followed the latter alternative, changing from time to time until finally they were specialized into the representatives of to-day. At the end of the Tertiary period the continents stood at a higher level than they do at present, and it is probable that a broad stretch of land connected Asia and North America. It was at this time, therefore, that the horse became cosmopolitan, and spread to the plains of all the continents except Australia.

The geological records of many families of animals and plants have been traced, but none so completely as that of the horse; and all such records lead to the same conclusion, that during the ages there has been a succession of evolutionary forms, leading by gradual stages to the animals and plants of to-day (Fig. 5).

II

EVOLUTION: ANATOMICAL AND BIOLOGICAL EVIDENCE

Anatomical evidence — Vestigial structures — Embryological evidence—Blood tests—Man a product of evolution.

WE have seen that geographical distribution and the study of fossils all demonstrate the truth of the doctrine of evolution, but besides these two important pieces of evidence there are others equally convincing which for lack of space can only be mentioned briefly.

Anatomical Evidence.—Prior to the publication of Darwin's book a great deal of study had been given to the structure of animal bodies. The various bones, muscles, nerves, blood vessels, etc., had been described and named in a great many species, but not until Evolution was being discussed did the science of Comparative Anatomy become important. Very soon, however, it was realized that certain structures of the bodies of different organism showed a great similarity one to another and were indeed homologous; that is, resembled each other in their architecture and corresponded to each other in their development. As an example let us take a series of fore limbs of some back-boned animals. The arm of a frog, the paddle of a turtle, the wing of a bird, the flapper of a whale, the wing of a bat or the arm of a man, though serving very different functions, are all built in the same pattern.

It is true that all are adapted in particular ways to their various uses, but in essentials these fore limbs are arranged on identical lines. Any interpretation of these facts is difficult other than the one which assumes that they are due to relationship.

Again it is found that the number of vertebræ in the necks of mammals is, with two exceptions, always seven; the long neck of the giraffe has exactly the same number of bones as the almost non-existent neck of the whale. Evolution readily explains this remarkable fact, but on no other theory is it explicable.

Vestigial Structures.—The English language, whose spelling is so different from its pronunciation, has many words, such as leopard, containing unsounded letters, which give a clue to the history of the word. In the same way in the bodies of animals there are found the remains of structures, now functionless, which give a proof of the animals' ancestries. The remains of the second and fourth digits in the legs of the horse are examples of such vestigial structures; also the tiny bones in the body of the whale, representing the hind limbs; and in the baleen whales the teeth which never cut the gums.

Embryological Evidence.—During the gradual growth from the egg to that of the perfect organism, it is often possible to find stages characteristic of adult creatures lower in the scale of life. For instance, fish obtain their oxygen from the water by their gill clefts. Reptiles, birds and mammals, however, have acquired an entirely new method of breathing through the lungs, yet during their embryonic development vestiges of the gill clefts always appear, though they can be of no possible use. A thoughtful reader will at once note here the interesting point that gill-breathing belongs to water life and will rightly infer that animal ancestry is to be traced back to an original habitat of shallow water. But in this connection it must be remembered that those mammals which have gone back to water life, the whales and dolphins, retain their lungs. The importance of this for Darwin's theory will be seen as we go on.

As a second example we may take the heart. In the fish this organ is two-chambered, it has an auricle which receives impure blood and a ventricle that drives it to the gills for purification. In the amphibia the auricle becomes divided into two, thus giving a three-chambered heart, while in the reptiles the ventricle is divided partially—except in the crocodile, where the division is complete and the heart is four-chambered. In birds and mammals the four-chambered heart with a right and left auricle and ventricle is the rule. During development, however, the hearts of mammals and birds pass through the stages outlined above ; there are the fish and amphibian heart stages in every developing mammal. In the same way other organs of the body, such as the kidneys and the brain, demonstrate by their development their evolutionary history.

Blood Tests.—One of the most complete proofs of the kinship of the various species of back-boned animals is given by the ingenious experiments of

Freudenthal and Nuttall. These men found that if the blood of a rabbit was introduced into the blood stream of a near relative, such as a hare, the two kinds of blood mixed freely together; but if the rabbit's blood was introduced into an animal not so closely related, as for example a dog, a definite antagonism was produced, causing the destruction of the red blood corpuscles. Numerous experiments of this kind have now been carried out, and the test forms a very reliable means of discovering the nearness of relationship between two animals.

It is impossible in a small volume of this kind to give more than the barest outline of the evidence for evolution, but for those who wish to follow this subject more deeply the bibliography given at the end of the book will be helpful.

Man a Product of Evolution.—That evolution is one of the foundation-stones of biology is indubitable, and is to-day generally admitted by all thinking people, whether scientists or not. But while accepted for the lower animals and plants, a reluctance is sometimes shown to believe that Man himself is a product of evolution. This is certainly the case, and some of the evidence must now be reviewed.

We have already seen that the developmental stages of an animal often shed a light on its evolutionary history, and the human body is no exception to the rule. As with all mammals, at a very early stage in its growth there appear in the region of the throat a series of slits or folds, which are homologous (that is, comparable in origin) with the gill slits of fishes. Such slits, being useless, rapidly disappear, except the first one, which becomes modified into the Eustachian tube—a passage leading from the throat to behind the ear drum and serving to keep the air pressure on each side of the drum constant. Additional evidence of man's remote kinship with fishes is afforded by the heart, which in its early stages is like that of a fish with arterial arches running to the gill clefts. Further, the nose first appears as a pair of depressions in the skin, connecting with the mouth by an open groove, as in the snout of the shark. These grooves then close and become nostrils, which further develop, by stages recalling the condition in the reptile, into the nose typical of man. The jaws, ears, limbs, etc., show an equally interesting development.

Vestigial structures abound in the human body, numbering, according to Metchnikoff, above a hundred. For instance, the ear in mammals may be regarded as a kind of hearing trumpet, which by means of muscles can be moved forwards or backwards to locate the direction from which a sound is coming. Our flattened ears are useless for such a purpose, but the old muscles for causing its movement are still present and two of them can be used by many people. The whole apparatus is useless, and only serves to remind us of our ancestors who possessed erect ears.

A second vestigial structure is found in the eye. At the inner corner of each eye there is a small red useless pad. It is the remains of a third eyelid, which still functions in birds to-day, as everyone can discover by watching a large bird and noting the film-like structure which is occasionally flicked across the eyeball from the inner corner. In our brain also there is a small body, the pineal gland, of no apparent function, but this is the remains of a third eye located at the top of the head of our reptilian ancestors.

The muscles enabling us to knit our brows are another example; these are the remains of a series covering the bodies of ancestors who were capable of keeping off flies by twitching the skin.

Probably it is no longer necessary to tell even the general reader, that man must not be considered as having evolved from any existing race of ape. Man and the apes have come from a common stock, but since the larger apes, such as the gorilla, orang-outang, etc., and man are, as it were, cousins, it is not surprising to find many structural similarities between them.

The skeletons of man and the anthropoid apes are in all essentials alike, though man's erect attitude has caused modification in the shape of the skull, foot, backbone, etc. In the apes the backbone is bow-shaped, while in man it is more like a reversed S, but in a baby the spine is curved as a bow for a long period, with the result that the baby crawls on all fours.

Before birth the body is covered with a fine coat of hair, which can only be regarded as a relic of our ancestor's natural covering only comparatively recently lost by us, for it was still well developed in prehistoric man. The direction of the hair on the arms is also instructive; generally it grows upwards and outwards, as in the apes. This can be understood when it is remembered that the apes during rain usually make a roof with their arms, and that by the direction of the hair the water is turned off their bodies.

Further evidence of our ancestry is afforded by the remarkable grasping power of the fingers and toes directly after birth, and by the characteristic attitude in which a baby sits on the ground with the knees bent outwards and the soles of the feet opposed to each other.

Lastly there is the evidence of the blood. Earlier in the chapter it was mentioned that the blood of two closely related species of animals showed no reaction when mixed. This test has been applied to man and the anthropoid apes, and the result has shown that the relationship between them is close.

It is impossible to follow here the history of man's evolution as it may be traced in the rocks, but sufficient evidence has been given to show that man cannot be regarded as having appeared suddenly in all perfection as by the waving of a magician's wand, but as the ultimate product of long ages of evolutionary change and progress.

III

EVOLUTION BEFORE CHARLES DARWIN

Early Greek theories — Linnæus — Buffon — Erasmus Darwin—Lamarck.

THE conception of organic evolution is often spoken of as originating in the nineteenth century through the work of Charles Darwin, and to a large extent this is correct; but the theory of evolution, as so often happens, was foreshadowed long before the publication of the "Origin of Species" in 1859, though never in so complete or convincing a way.

In order to gain perspective by viewing the subject from as many different angles as possible consideration should be given to the history of the idea, demonstrating the growth of the theory.

Early Greek Theories.—It is extremely interesting to read the views of the ancient Greeks on the idea of evolution, and surprising to find them in many ways foreshadowing what we regard as the typical nineteenth or twentieth century discovery. Five centuries before the Christian era we find Anaximander dealing with the problem, and in Empedocles (495–435 B.C.) we have the father of Darwinian Evolution, for his teaching was not merely that of a relationship between the different species of animals, or plants, but that nature was continually trying new types, some of which were better fitted to their environment, others which —less fitted—died because of their inferiority. In fact we have the idea of the survival of the fittest.

Other outstanding figures of that remarkable age were Heraclitus, who believed that all things were in a state of continual change, and Democritus. But by far the most remarkable of them all was Aristotle, the founder of the genuine scientific method and father of Natural History.

Born at Stagira, in Macedonia, in 384 B.C., he spent the early part of his life at Athens studying under Plato, and, as was the habit of scholars of his time, he covered a wide range of subjects ; there are historical records of some three hundred works which are attributed to him. He is sometimes regarded as a great classifier, and undoubtedly much of his time was so spent, but classification must only be considered as incidental ; much more important and more firmly established was Aristotle's work on the structure and development of animals—he was essentially a morphologist, that is a student of the forms of animals and their parts.

From our point of view, however, Aristotle must be remembered because of his ideas on the development of animals and plants in terms of time. He believed in a gradation from the lowest organisms to the highest : and that man was the highest point of one long and continuous ascent.

Space does not permit detailed consideration of the views of the various Greek philosophers concerning the origin of species, but they may be epitomized under three headings ·

(1) Intelligent design.
(2) Operation of natural laws as ordered by intelligent design.
(3) Operation of natural causes due to laws of chance.

Looking back it does indeed seem strange that these men of old were thinking on lines so similar to those followed by students of comparatively recent times.

But now a curious thing happened. One would have imagined that after such a stimulus as that given by the Greeks the idea of evolution would have spread widely, but that is not the case. It is true that it spread from the Greek to Latin culture, as witness the writing of Lucretius and the Plinys ;[1] or again references in the great Christian writers from St. Paul onwards to St. Augustine, and amongst the sixth century clerks of monastic libraries. The fact remains, however, that not until the coming of such men as Linnæus, Buffon, Erasmus Darwin, Lamarck and Charles Darwin was real progress once more made ; and from then onwards the advance never ceased.

Linnæus.—This great Swedish naturalist was born in 1707 of lowly stock. His father was a clergyman in a small village, and intended his son to follow the same profession. In spite of limited means the boy

[1] Students of history will remember how completely the high civilization of Greeks and Latins disappeared with the collapse of the Roman Empire. For close on a thousand years the focus of culture was shifted to the East, and for the Moors all nature was a tainted and dangerous thing, and this attitude had considerable influence on the feeble struggles of learning to survive in the wild west.

Traces of the idea of evolution crop up from time to time in the realm of the " philosophies," but the field of nature was shut off, and for at least half a millenium those who studied it were regarded as " suspects " at the least, often they were persecuted as heretics.

was sent to a good school, but gave no sign of scholarship and received unsatisfactory reports from his teachers. How strangely reminiscent this is of Charles Darwin's early days, for we learn that Linnæus spent all his time collecting natural history specimens.

Disappointed at his son's lack of progress in his work, the father reluctantly gave up the idea of the young Linnæus taking Orders, and decided that he should study medicine. With difficulty a small sum of money was raised, enabling the young man to go to the University of Lund, and then to Upsala. Extreme poverty prevented his taking a degree, however, and after leaving the University he went on an expedition to Lapland to collect specimens at the request of the Royal Society of Upsala, but on his return his financial difficulties were as great as before.

He decided once again to make an effort to obtain his medical degree and settle down as a practitioner, a resolve that was strengthened by his fiancée's father, who refused to give consent to his daughter's marriage until Linnæus had established himself. Again a small sum of money was scraped together, and in 1735, when twenty-eight years of age, he succeeded in getting his degree at the University of Hardewyk, in Holland.

Even then, however, he took no steps to become a practitioner, but instead continued his botanical studies at Leyden. Here he met many well-known men of science and began to establish that reputation which eventually was to place him in the front rank of naturalists.

Linnæus is best known for his classification of plants and animals; he was throughout a firm believer in the origin of species by "Special Creation," though he admitted the production of "post-creation" forms by hybridization. As a contributor of facts on which later students were to build Linnæus will always be remembered, and his work, by fixing attention upon species, proved a great stimulus to research along evolutionary lines.

Buffon.—This French savant was born the same year as Linnæus, but the upbringing and early life of the two men were very different. Linnæus, a poor student always struggling to supply his scanty needs, while at the same time acquiring his extensive knowledge of natural history; Buffon, a man of elegance, with an assured position in society and able to command attention for his work. He was a delightful writer, a circumstance that enabled him to make natural history popular; indeed it is said that the advance sheets of his "Histoire Naturelle" were to be found in the boudoirs of ladies of fashion.

As an investigator Buffon does not rank high, for he left few original contributions to science; his mind was philosophically rather than scientifically inclined.

There is no doubt that he was a firm believer in the process of evolution, but he lived in times of rigid ecclesiastical authority, when it was not wise to express decided views on a subject so distasteful to the Church as evolution. Further, as Lull says, "he was not of the stuff of which martyrs are made."

To Buffon environment was all-important as modifying the structure of animals and plants, and he believed the modifications so produced were inherited. He was wise enough not to state this in so many words, but his writings leave little doubt that this was his belief. On one point he was definite, namely, that overcrowding was prevented by the struggle for existence, herein anticipating Malthus, whose work on human population made so great an impression on Charles Darwin.

Erasmus Darwin (1731 – 1802).—This country physician and naturalist, the grandfather of Charles Darwin, was the greatest of Lamarck's predecessors. In 1794 he published a book, "Zoonomia," in which he stated ten principles regarding the course of evolution. Though his work was given recognition by thoughtful men, yet it soon passed into neglect, probably owing to the great popularity of Paley's book, "Natural Theology," which was written to counteract it, and also on account of the views of Buffon.

Erasmus Darwin's views differed from those of Buffon in that the influence of the environment in causing modifications was not emphasized. The variations of animals and plants, according to his concept, sprang from changes within the organisms themselves and were inherited. Thus he writes: "All animals undergo transformations, which are in part produced by their own exertions in response to pleasures and pains, and many of these acquired forms are transmitted to posterity." The check to the rapid increase of life by the struggle for existence was also clearly stated.

In many respects Darwin's views were very similar to those of Lamarck, indeed so much so that the suggestion has been made that Lamarck was directly influenced by them. Careful consideration of the matter, however, leads to the conclusion that Lamarck drew his inspiration directly from nature and that the similarity between the two views is an example of parallelism of thought.

Lamarck (1744–1829).—We now come to a man whose influence on the theory of evolution is second only to that of Charles Darwin, indeed by some modern biologists his theories are accepted, while those of Darwin are discredited. Without doubt Lamarck was a remarkable man, of brilliant intellect. Like Linnæus, his early life was a struggle against poverty, rendered all the harder on account of the lack of recognition paid to his work by his contemporaries, and in later life by complete blindness. This was, however, rendered bearable by the devotion of his daughter Cornélie, who encouraged him by constantly predicting that posterity would recognize his work. He was a member of a large family, being the eleventh child. His brothers all entered the army, following a profession which was traditional to the Lamarcks. Jean Baptiste, however, was intended for the Church, although against the boy's wish ; and he was sent to a Jesuit College at Amiens. Here he remained until seventeen years of age, when his father died.

Theology was as distasteful to him as ever, so he decided to leave the college and join the army, which was fighting in Germany. He managed to procure a broken-down horse, and, with a letter of introduction to the colonel, arrived on the scene of action. Largely owing to his importunity, for the colonel was not favourably impressed by this latest recruit, Lamarck attained the rank of sergeant. His first engagement was a particularly hot one ; all the officers were killed, and Lamarck found himself in command of the fourteen remaining grenadiers.

The retreat of the army had been ordered, but such was Lamarck's independence and courage that he refused to move until the order had been sent to him direct.

His adoption of the study of natural history as a life work was due to the result of an accident, by which he was unfitted for military life ; he went to Paris to study medicine and while doing this became interested in botany, to which study he remained attached until 1794, when he was fifty years of age. He was then Professor of Botany in the Jardin des Plantes, but consented to take charge of the department of invertebrates, and changed from the study of plants to that of animals. This change had a profound influence in shaping his ideas.

" All that Lamarck had written before he changed from botany to zoology indicates his belief in the fixity of species, which was the prevailing view of the day. Then in 1800 he expressed a contrary opinion, to which he held unwaveringly to the close of his life."

His theory was that modifications, that is variations, in the structure of plants and animals were due to some force exercised during their life. In the case of plants, environment was the chief agent ; thus soil conditions, altitude, moisture, heat and light were important factors inducing variations which were inherited. The shape of irregular flowers was supposed to have been caused by the strains induced by the visits of bees and other insects during their search for honey. In stressing the action of environment Lamarck agreed with Buffon.

In the case of animals Lamarck regarded the environment as undoubtedly playing a part, but considered that the most fruitful cause of variation arose from the effect of use and disuse. As a consequence of the ever-changing conditions under which an animal lived, the animal's needs (*besoins*) were always changing. Continual striving to satisfy these "needs" would cause a change in the habits of the animals, involving extra use of some particular organ or structure or disuse of some organ or structure. This would mean a modification in the shape or build of the body, for structures become developed through use, and diminished, with loss of power, by disuse. Such modifications would be of little importance unless transmitted from generation to generation; but according to Lamarck they are strongly inherited, as shown by his second law:—"Everything which nature has caused individuals to acquire or lose by the influence of circumstances to which their race may be for a long time exposed, and consequently by the influence of the predominant use of such an organ, or by that of the constant lack of use of such part, it preserves by heredity and passes on to the new individuals which descend from it, provided that the changes thus acquired are common to both sexes, or to those which have given origin to these new individuals."

One or two examples, which Lamarck himself used, will explain his theory more clearly than any description.

The majority of back-boned animals have two pairs of limbs, but the snakes are characterized by lacking any visible sign of such structures. Lamarck supposed that snakes were descended from animals, thin in shape but having two pairs of limbs. These animals acquired the habit of gliding over the ground and concealing themselves in the grass; owing to their repeated efforts to elongate themselves so as to pass through crevices, the bodies became more and more elongate, and as such modifications were inherited the thin shape of the snake would be established. During this process of evolution the limbs would serve no purpose and would not be used. Hence they would gradually, through disuse, become smaller and smaller, finally disappearing completely.

Similarly the giraffe with its long neck was supposed to have been derived from short-necked ancestors who acquired the habit of browsing on the leaves of trees growing in arid regions. This would necessitate a constant stretching upward, resulting in a slight increase in the length of the neck. Such increases, being accumulated by inheritance, ultimately led to the giraffes of to-day.

Other examples of the effect of use are given by Lamarck as follows :—" A bird driven through want to the water to find the prey on which it feeds will separate its toes whenever it strikes the water, or wishes to displace itself on its surface. The skin uniting the bases of the toes acquires, through the repeated separating of the toes, the habit of stretching, and in this way the broad membrane between the toes of ducks and geese has acquired the appearance we observe to-day. Similar efforts to swim, that is to repel the water and move in it, have stretched the membranes between the toes of frogs, sea turtles, otters, beavers, etc. Likewise the shore birds, which do not care to swim, but must approach the water in order to obtain food, are continually in danger of sinking into the mud ; but wishing to act so that their body shall not fall into the liquid, they try their best to extend and lengthen their legs. Owing to the habit those birds acquire, of extending and lengthening their legs, they find themselves raised as it were upon stilts, having gradually grown long legs, bare of feathers up their thighs or even higher."

From the above it will be easily recognized that Lamarck's theory depends on the assumption that acquired characters, that is, bodily characters acquired during the life of the organism as a response to changes in its environment, are inherited. All students of biology of this period held this theory, and it was accepted by Charles Darwin himself. During the last fifty years, however, the belief has steadily grown that such characters are not inherited, but discussion of this may well be deferred to a future chapter.

Whether Lamarck's views are true or false, however, it must be remembered that he was the first to give a theory of the method of organic evolution that has retained a place in the intellectual world up to the present time, for his ideas regarding the beginnings of variations have been revised and accorded respect under the designation of "Neo-Lamarckism."

With Lamarck our sketch of the history of evolutionary thought up to the time of Charles Darwin is ended. Space does not admit of dealing with work except that of the three old masters, as they may be termed, Buffon, Erasmus Darwin, and Lamarck. There were, however, other quite convinced evolutionists, such as Etienne Geoffroy Saint-Hilaire, Goethe, Treviranus, and Robert Chambers, indeed Darwin refers in his historical sketches to thirty-four writers on evolution.

Our purpose has been to show that the theory of evolution did not as it were burst upon the world as a result of the labours of Charles Darwin, but was, like most great ideas, of slow and gradual growth. At the same time it cannot be too strongly insisted upon that Darwin did not simply continue the work of his predecessors, for during the early years when he was collecting material for his great book he knew little or nothing of what had been previously written on the subject.

IV

CHARLES DARWIN AND EVOLUTION

Biographical sketch—Darwin and Wallace—Survival of the fittest and natural selection—Example of natural selection.

WE now come to the culminating point in the history of the progress of evolution, and must consider the views developed by that greatest of all naturalists, Charles Darwin. He was born at Shrewsbury on February 12, 1809, the birthday also of Abraham Lincoln.

As Prof. Arthur Thomson has pointed out, this was indeed a year remarkable for the greatness of its children, for it saw the birth of Gladstone, of Chopin and Mendelssohn, of Edgar Allan Poe, of Edward Fitzgerald, of Oliver Wendell Holmes, and of many others who became famous.

The Darwin family is an example of inheritance of mental capabilities. Charles Darwin was the grandson of Erasmus Darwin, the author of the famous book, "Zoonomia"; his father, Robert Waring Darwin, was a physician, possessing an unusually keen faculty for observation; and his mother was the daughter of Josiah Wedgwood, the founder of the famous pottery works. Also it may be noted that Sir Francis Galton, the founder of the science of Eugenics, was Darwin's cousin, while all of Darwin's sons have attained positions of eminence in the scientific world.

Darwin's early years gave no indication of his extreme intellectual ability. After leaving school he and his brother proceeded to Edinburgh University to study medicine, but the work did not interest him, for he found the lectures "incredibly dull," and made little progress. At the end of two sessions he left Edinburgh and proceeded to Christ's College, Cambridge, to study theology prior to entering the Church. During his three years' residence he did sufficient work to enable him to take a degree, but most of his time was spent in natural history pursuits and scientific study, in which he was encouraged by the professor of botany, Henslow. The turning point in Darwin's career came after taking his degree. He was appointed naturalist on the "Beagle," which was going on a surveying expedition under the command of Captain Fitz-Roy. In his autobiography Darwin relates the amusing incident that he was nearly refused appointment because Fitz-Roy doubted "whether a man with such a shaped nose could possess sufficient energy and determination for the voyage."

The voyage lasted from 1831–1836, and Darwin was able to make many expeditions and to collect much valuable material. During the expedition to the Galapagos Islands his thoughts were turned to the question of the origin of species, and he opened his first note-book on the subject in 1837, after the return of the "Beagle."

Subsequently Darwin bought a house at Down, and continued his researches in all branches of natural history. The amount of work he did was remarkable, and when it is remembered that for the rest of his life he was a semi-invalid one is lost in admiration at his tenacity of purpose. His illness involved constant sickness and giddiness, so that "for nearly forty years he never knew one day of the health of an ordinary man, and thus his life was one long struggle against the weariness and strain of sickness. Under such conditions absolute regularity of routine was essential, and the day's work was carefully planned out. At his best, he had three periods of work: from 8 to 9.30, from 10.30 to 12.15, and from 4.30 to 6, each period being under two hours' duration."

For twenty years Darwin collected evidence regarding the origin of species before making any statement of his views, for it was not until 1858 that his first paper was published; and it is doubtful if even then he would have published had it not been for a curious circumstance.

Wallace.—In that year Darwin received from Alfred Russell Wallace, then a young naturalist collecting in the tropics, a letter, asking him to read and criticize the theory Wallace had come to concerning the origin of species. To Darwin's surprise he found that the theory was practically identical with his own.

With characteristic generosity, almost unbelievable in these days of commercialized science, Darwin proposed to withdraw all claim, and to publish Wallace's essay without reference to his own work. Happily, however, the advice of two friends, Hooker and Lyell, prevailed, and a joint paper in the names of Darwin and Wallace was read before the Linnæan Society in London in 1858. Then, in the following year, the great book, "The Origin of Species," was published.

Wallace's letter arrived at a sad time for Darwin—he was very ill, and the day previously one of his children had died from scarlet fever, and another was ill with diphtheria. Darwin at once wrote to Lyell, enclosing Wallace's communication, and said, "I never saw a more striking coincidence; if Wallace had my MS. sketch written out in 1842, he could not have made a better short abstract! Even his terms now stand as heads of my chapters. Please return me the MS., which he does not say he wishes me to publish, but I shall, of course, at once write and offer to send to any journal. So all my originality, whatever it may amount to, will be smashed, though my book, if it ever has any value, will not be deteriorated, as all the labour consists in the application of the theory. I hope you will approve of Wallace's sketch, that I may tell him what you say."

Nothing could be more generous than the attitude Wallace adopted in the affair. He entirely agreed with Lyell and Hooker's decision to publish a joint paper, and in 1870, when Darwin's fame was established, he wrote, "I have felt all my life, and I still feel, the most sincere satisfaction that Mr. Darwin had been at work long before me, and that it was not left for me to attempt to write 'The Origin of Species.' I have long since measured my own strength, and know well that it would be quite unequal to that task. For abler men than myself may confess that they have not that untiring patience in accumulating, and that wonderful skill in using large masses of facts of the most varied kind,—that wide and accurate physiological knowledge,—that acuteness in devising and skill in carrying out experiments,—and that admirable style of composition, at once clear, persuasive and judicial, —qualities which in their harmonious combination mark out Mr. Darwin as the man, perhaps of all men now living, best fitted for the great work he has undertaken and accomplished."

And fifty years after the publication of the theory of Natural Selection he said at the Linnæan Society, "I was then (as often since) the 'young man in a hurry,' he (Darwin) 'the painstaking and patient student,' seeking ever the full demonstration of the truth he had discovered, rather than to achieve immediate personal fame."

On reading the accounts given by these two men as to the way they arrived at their conclusions, remarkable parallelism of thought is found, and curiously enough the same book, Malthus' "On Population," gave to both of them the idea of Natural Selection. Darwin's account runs: "In October, 1838, that is, fifteen months after I had begun my systematic inquiry, I happened to read for amusement 'Malthus on Population,' and being well prepared to appreciate the struggle for existence, which everywhere goes on, from long-continued observations of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here, then, I had at last got a theory by which to work, but I was so anxious to avoid prejudice that I determined not for some time to write even the briefest sketch of it. In June, 1842, I first allowed myself the satisfaction of writing a very brief abstract of my theory in pencil, in thirty-five pages, and this was enlarged during the summer of 1844 into one of 230 pages."

And Wallace gives this account: "In February, 1858, I was suffering from a rather severe attack of intermittent fever at Ternate, in the Moluccas; and one day, while lying on my bed during the cold fit, wrapped in blankets, though the thermometer was at 88° Fahr., the problem again presented itself to me, and something led me to think of the 'positive checks' described by Malthus in his 'Essay on Population,' a work I had read several years before, and which had made a deep and permanent impression on my mind. These checks—war, disease, famine, and the like—must, it occurred to me, act on animals as well as man. Then I thought of the enormously rapid multiplication of animals, causing these checks to be much more effective in them than in the case of man; and while pondering vaguely on this fact there suddenly flashed upon me the idea of the survival of the fittest—that the individuals removed by these checks must be on the whole inferior to those that survived. In the two hours that elapsed before my ague fit was over, I had thought out almost the whole of the theory; and the same evening I sketched the draft of my paper, and in the two succeeding evenings wrote it out in full, and sent it by the next post to Mr. Darwin."

There are three fundamental principles underlying Darwin's theory, variation, heredity and Natural Selection, the last being the central pivot of the whole idea.

Variation.—The members of a family are not all alike at birth. They vary one from another; and though they may grow to maturity under the same conditions, yet the differences will remain. Any one who has made collections of animals or plants will have noticed variation between members of the same species. All are in general appearance similar, but in detail of colour, structure, etc., each will differ to some extent from its fellows. The differences may be large or small, but they are definite. Since Darwin's time the amount of such variation among living things has been found to be much greater than was supposed. Lamarck's theory demands an explanation of the origin of variation; but this was not necessary for Darwin, who frankly said he did not know how they arose.

Heredity.—Again, as with variation, we are dealing with an established fact. It is sufficient to point out that many of the variations found in animals or plants will be passed on from one generation to the next. It is necessary that this should be so for the Darwinian theory; but whether the type of variation known as an acquired character is inherited or not in no way affects it. Darwin himself believed such characters might be inherited: a view not widely held to-day; but it cannot be too strongly stressed that the ultimate settlement of the question will not materially alter the Darwinian theory.

Natural Selection.—Those animals or plants, which have been the special study of mankind, either for their food qualities or other valuable characteristics, exhibit a vast variety of forms, as for instance the various breeds of poultry and strains of wheat, barley, etc. These varieties have been produced by the deliberate action of breeders, who have kept a look out for novelties which Nature has sent them and have then bred from them. Of the resulting offspring those which do not conform to the standard desired have been discarded, while those which have the characteristics, to the same or to a higher degree, for which their parents were preserved have been kept to produce the next generation. In other words, the breeder keeps the forms which he desires and destroys the rest. This is artificial selection. Its action is simply preservative or destructive.

The great changes which in this way could be produced in domesticated animals and plants impressed Darwin, and he began to look for some similar operation occurring in Nature.

The numbers of individuals composing any species of animal or plant are relatively constant, but the rate of increase is often very great. Prof. Punnett, when experimenting with a Rotifer, an animal so small as to be barely visible, calculated that if, after sixty-seven generations, which were produced in about a year, he had been able to rear all the animals from all the eggs produced the total mass would have formed a sphere greater than the earth.

As an example of the rate of increase of a highly developed animal we may take Darwin's own instance. Assuming that the elephant first breeds at thirty years of age, and lives to the age of one hundred, and during the interval has six young, then if all the animals survived, for their natural period of life, after 740–750 years there would be about 19,000,000 elephants descended from the original pair.

In view of such facts it is evident that in Nature there must be some factor keeping down numbers. It is not difficult to discover what this factor may be.

Since the space and food supply available for all animals and plants are limited, it follows that there must be a proportion of them that are killed before reaching maturity. There is, in fact, a struggle for existence.

"It occurs between organisms of the same species: between friends and foes, and between living creatures and their environments, with the inevitable result that the numbers are reduced and increase in population is checked.

"Now since variability is a fact of life, some members of a family will have certain characters rendering them better able to meet the struggle for existence, while others are less able to do so; these latter, being less fitted to get their food and to leave large families, will in the course of time be eliminated. In this way there will eventually be built up a race of animals or plants adapted to their surroundings; and further, the severer the struggle, the more perfect will be the adaptation."

Darwin's own exposition of Natural Selection is as follows:

If under changing conditions of life organic beings present individual differences in almost every part of their structure, and this cannot be disputed; if there be, owing to their geometrical rate of increase, a severe struggle for life at some age, season, or year, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of life, causing an infinite diversity in structure, constitution and habits, to be advantageous to them, it would be a most extraordinary fact if no variations had ever occurred useful to each being's own welfare, in the same manner as so many variations have occurred useful to man. But if variations useful to any organic being ever do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life ; and from the strong principle of inheritance, these will tend to produce offspring similarly characterized. This principle of preservation, or the survival of the fittest, I have called Natural Selection. It leads to the improvement of each creature in relation to its organic and inorganic conditions of life, and, consequently, in most cases, to what must be regarded as an advance in organization. Nevertheless, low and simple forms will long endure, if well fitted for their simple conditions of life.

Confusion has sometimes arisen from a mistaken notion that Natural Selection is an active process ; that Nature deliberately selects certain characters as breeders do in domesticated animals and plants. This is of course not the case. Natural Selection is a passive agent, it cannot create, it can only destroy or preserve. It is the inevitable outcome of the interaction of variation and the struggle for existence by which the fittest survive.

Also it is important to realize that the struggle for existence does not necessarily mean the sudden elimination of the unfit. If they have smaller families than their superior fellows, or if they are unable to give the necessary attention to their offspring, then in the course of time they will be destroyed. Geological evidence exists in plenty for gradual disappearance of species and groups.

The effect of Natural Selection as an evolutionary process, as Lull summarizes it, is :

(*a*) Under new conditions harmful characters will be eliminated by selection.
(*b*) Beneficial characters are intensified and modified.
(*c*) The great body of characters neither harmful nor beneficial will not be modified, but will persist through heredity.

Examples of Natural Selection.—For those who wish to go more deeply into the effect of Natural Selection recourse must be had to the numerous books that have appeared : here it is impossible to give more than two examples, both of which are taken from Darwin.

The sharp eyes of the hawk have arisen by Natural Selection eliminating hawks born with weak or defective vision, because they could not see their prey and get sufficient food. In this manner a race of birds has appeared possessing keen eyesight and this standard of vision is maintained.

Thus Natural Selection tends to adapt animals to their environment, not always by increasing the efficiency of an organ, as in the above case, but sometimes by decreasing it. According to Darwin the race of short winged beetles found on certain oceanic islands is due to the fact that the original beetles with normally developed wings would, while flying, be carried by the high winds into the sea and perish. Because of variation, however, beetles with poorly developed wings are perpetually arising which would be preserved because of their inability to fly, and consequent protection from the wind. Thus generation after generation the strong-winged beetles would be eliminated, and a race of short-winged forms built up.

Since Darwin's day there have been one or two further demonstrations of the action of Natural Selection; it has been possible actually to see the process at work. The best known example is that of the praying Mantis (*Mantis religiosa*). In Italy there are two varieties of this insect, one coloured green, living in the grass, the other brownish, found on withered foliage. An Italian naturalist decided to test the action of Natural Selection in the following manner: Twenty green Mantes were tethered on grass and twenty brown ones on withered grass: after seventeen days all the insects were alive. He then placed twenty-five of the green variety on brown herbage, and after eleven days all were dead; while out of forty-five brown insects exposed on green grass only ten were alive after seventeen days. The deaths were due to the attacks of birds or ants. This was one of many experiments demonstrating that selection does occur. If green and brown Mantis were both placed in green surroundings in a very short time the brown variety would be eliminated.

Another example is given by Prof. Arthur Thomson. During the August of 1909 a heavy snowstorm occurred at Johannesburg, destroying many trees by the weight of snow on the branches. It was interesting to note that the destruction was largely selective. The trees most affected were the imported Blue Gums and Black Wattles, possessing soft wood and abundant foliage. The Deodars from the Himalayas, however, were scarcely affected, doubtless owing to their having pendulous branches and needle-shaped leaves from which the snow could slide.

These two examples are important in showing that the possession of certain characteristics, apparently unimportant, may make all the difference between life and death. Nor is it necessary for a population to contain large numbers of a new advantageous variety for it to dominate; for as Prof. Punnett has shown, "if a population contains ·001 per cent. of a new variety, and if that variety has even a 5 per cent. selection advantage over the original form, the latter will almost completely disappear in less than a hundred generations."

A theory, if it is of any value, is amplified or modified as knowledge increases: and so it is with Natural Selection. Darwin believed in the inheritance of acquired characters; as will be seen in a later chapter, most modern biologists do not accept this view, but in the opinion of the present writer the main theory of the origin of species by Natural Selection stands as firmly to-day as ever.

V

LAWS OF HEREDITY

Mendel's laws—Inheritance of simple "crosses."

THE time has now come to take up the question of heredity, but before doing so it will be well to point out one or two characteristic features in the life of an animal or plant. If we trace the life-history of an organism it is apparent that in the early stages of its formation, when there are still so few units that they may be readily counted, the differentiation of the layers forming groups of tissues takes place; amongst these the germ cells are of prime importance: the cell or cells, split off in this early phase of development, are spoken of as reproductive tissue, or more technically germ plasm.

This point brings us necessarily to a review of the phenomenon of bi-parental reproduction, entailing fertilization or cell-fusion. The bald fact is familiar to everyone in such everyday occurrences as the distribution of pollen for the "getting" of seed in the female egg-cell, or ovule of the flower. Here it is more important, for a true understanding of the evolutionary aspect, to draw attention to the fact that numerous primitive forms exist in which the reproductive tissue, by its division, sheds cells that divide without fertilization to form the new individual.

The process, however, which characterizes all the higher forms of life, both plant and animal, is that in which two cells derived from the reproductive tissue of distinct sexes fuse before the initiation of the divisions entailed in the development of the new individual. This fused unit we may describe as the egg-cell, whether it be the seed of a plant or the embryo of an animal.

The review of breeding experiments which follows shows the result of fertilization of the larger female cell by the small active male cell (" pollen " in plants, " sperm " in animals) where both male and female reproductive tissues exist in the same individual, contrasted with the result of fertilization of cells from different individuals, and further of a fusion between germ cells of individuals differing markedly in character—commonly spoken of as " crossing " or " hybridization."

The Work of Mendel.—This had formed the basis of a great deal of research before the time of Charles Darwin, but the foundation of modern work was laid by an Austrian monk, Mendel (1822–1884), the abbot of Brunn monastery. He published papers in 1866 and 1867, but the scientific world was so occupied with discussing the " Origin of Species " that Mendel's work was overlooked. It is interesting to speculate what effect the discoveries would have had on Darwin, had he known of them.

But the observations remained unknown until 1900, when Correns, and later Tschermak, repeated Mendel's experiments and brought his work to the notice of scientists. Since then investigations have proceeded in every part of the civilized world, and yearly there appears a flood of literature showing the universality of Mendel's laws.

There had been before Mendel many naturalists who had crossed different species of plants and studied the hybrids so produced, but the work did not meet with conspicuous success. This was no doubt partly because they took the plant as a whole, and did not confine their observations to single discrete characters. It is the essence of the Mendelian method to study as separate units obvious striking characteristics of an animal or plant.

As previous workers did not do this there had grown up the belief that hybrids were usually intermediate between their parents, resembling the one parent in this character, and the other parent in that, but following no obvious law.

Mendel chose as his material for the early experiments the common edible pea. This has two advantages; firstly, its flowers can be self-fertilizated, (i.e. the pollen can be used to fertilize the ovule of the same flower); and, secondly, it possesses numerous well-marked varieties, easily differentiated one from another, e.g. green or yellow coloured seed coats; round or wrinkled seeds.

Such characters Mendel decided to investigate, and made a large number of crosses between parent plants possessing one or more such distinguishing features.

As an example of one of these experiments a cross between two varieties, one breeding true to yellow seeds and the other to green seeds, may be given.

If the pollen from the flower of the yellow variety be transferred to the stigma of the green one (or vice versa, for the result is the same in both cases), the seeds will not be intermediate in colour, but yellow. If plants are raised from these seeds and the flowers self-fertilized, or crossed with plants having a similar ancestry, the peas formed, instead of having all yellow seeds, are found to possess both yellow and green in the proportion of 3 : 1. Further breeding shows that the green seeds breed true to type, but that of the yellows one-third breed true, and the remainder give

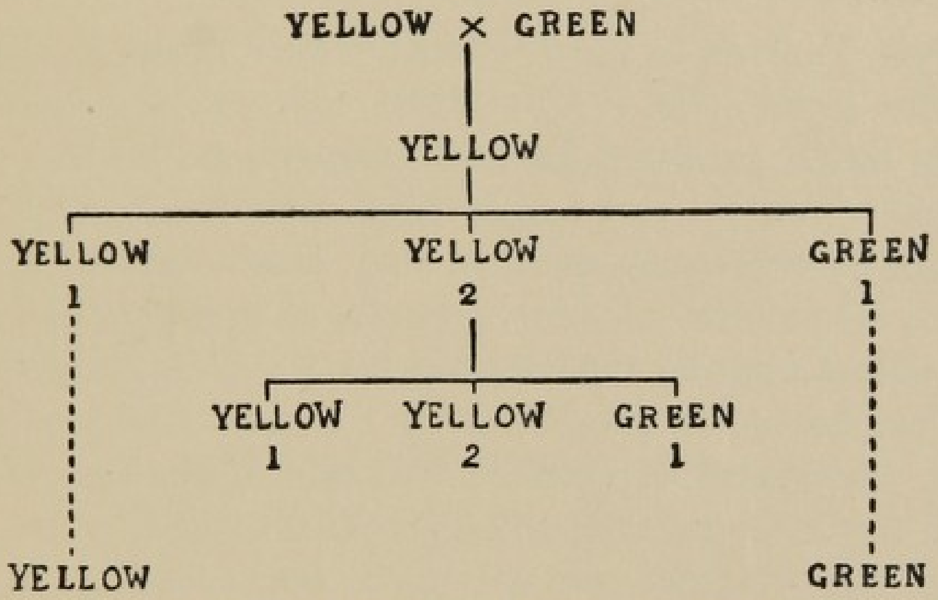


Fig. 6.—Inheritance of yellow and green seed coats in the pea.

yellows and green in the same ratio as before, 3 : 1. This is illustrated in Fig. 6.

In the same way similar crosses between tall and dwarf varieties of sweet peas give in the first generation (technically termed F_1, or first filial generation) all tall plants, and in the second (F_2) generation three tall and one dwarf. The dwarf plants breed true, as do also one-third of the tall plants, the remainder giving talls and dwarfs in ratio 3 : 1 (Fig. 8).

Yellow and green were regarded by Mendel as alternative characters, and since yellow alone appears in the F_1 generation he termed it dominant while green, which is masked by crossing with dominant, he called recessive.

The explanation of the results is that the factors for the characters are carried by the germ cells (pollen and ovules in the case of plants, sperm and ova in the case of animals), which are of two kinds, one kind bearing the dominant, the other the recessive, of any alternative pairs and in equal numbers.

Unit Factors.—An illustration will make it clearer. In the germ cells the material representing yellow or green seeds is termed for convenience a factor or a gene, terms which do not imply any knowledge as to the nature of substance causing such characters to appear in the adult plants. For the sake of brevity the factor for yellow may be represented by Y: that for green y.

The plants are produced by the union of two germ cells, and therefore contain two sets of characters, one from the male parent, the other from the female.

As the original plants used for crossing in the experiment were known to breed true to type, the yellow factor or the green factor must have been present in both germ cells forming the plants. The yellow and green parents may, therefore, be represented as YY and yy (Fig. 7).

The plants from these seeds will in their turn form germ cells, those from the one parent containing the factor Y and those from the other the factor y. Union between these germ cells will result in plants having the constitution Yy, that is yellow seeded, for yellow is dominant to green. It should be noted that these yellows, though in appearance like their yellow parent, are, as regards factorial constitution, different.

The F_1 plants will in turn give rise to germ cells, half of which carry the factor Y and half the factor y, but never does a germ cell contain both factors. If there is an equal chance of a pollen grain fertilizing an ovule containing the same or the alternative factor to that which it bears, then it follows that the individuals of the next generation will be in the proportion of three

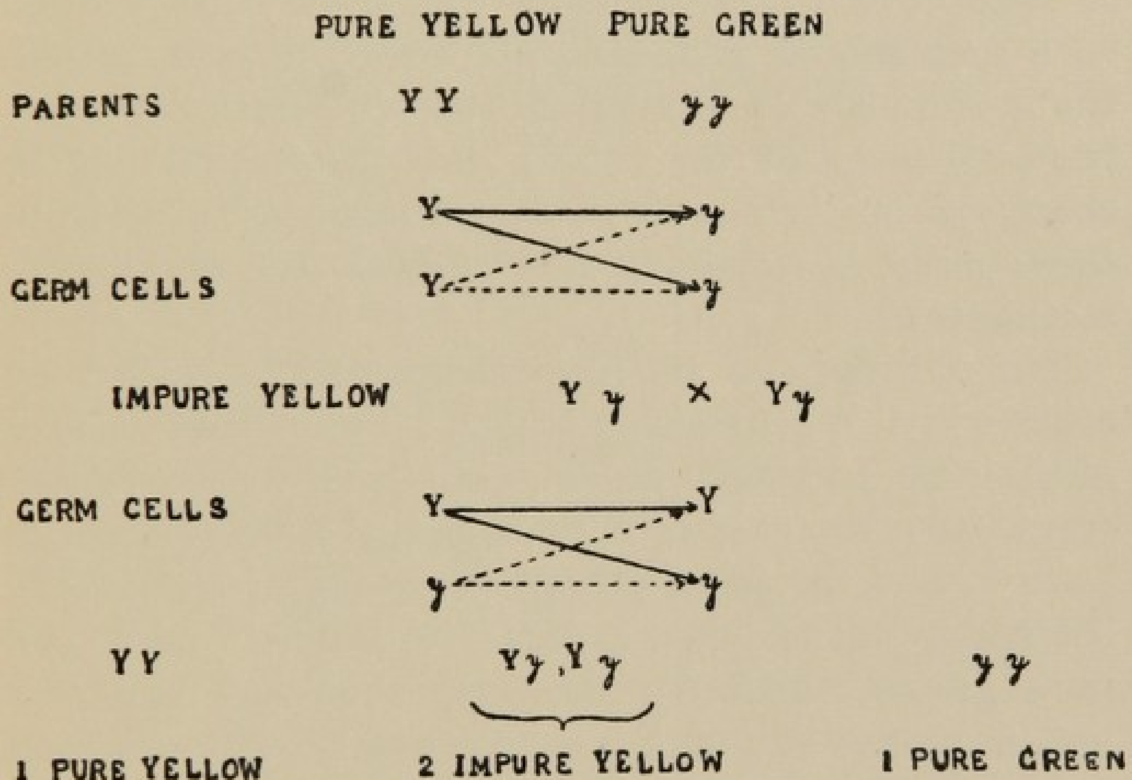


FIG. 7.—Factorial explanation of the inheritance of yellow and green seed coats.

yellow to one green. For Y may fertilize Y or y, giving YY or Yy, both yellow plants; and y may fertilize y or Y, giving yy or yY, as shown in Fig. 7. Since YY and yy plants are pure in respect of the factors they can give rise only to yellow and green seeded varieties respectively. This condition is known as "homozygous." The Yy plants, on the other hand, are impure, for they contain both factors and are called "heterozygous."

This idea of the segregation of the dominant and recessive factors into two different sets of germ cells is the foundation of the Mendelian theory. As Mr. Bateson has said, " The essential part of the discovery is the evidence that the germ cells produced by cross-bred organisms may in respect of given characters be of the pure parental types, and consequently incapable of transmitting the opposite character: that when such pure similar germ cells are united in fertilization, the individuals so formed and their posterity are free from all taint of the cross: that there may be, in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters."

The accuracy of the hypothesis can be tested by crossing back the first generation hybrid with either of the pure parental types: since the hybrid produces germ cells fifty per cent. containing Y and fifty per cent. y, and the green parent forms only y germ cells, the result will be equal numbers of impure yellow and pure green. Similarly the hybrid crossed with the yellow parent will give rise to equal numbers of pure yellow (YY) and impure yellow (Yy).

Mendel tested these expectations by experiment and found they were verified.

A second example of the mode of inheritance of alternative characters is given by the tall and short varieties of pea. The cross of pure talls and shorts results in the production of impure talls, which when crossed together give in the next generation pure talls, impure talls and pure shorts in the proportion of 1 : 2 : 1. Calling the factor for tallness T and that for shortness t, the scheme is given in Fig. 8

In these two examples the dominant character completely masks the recessive one; this is, however, not always the case.

For instance, the garden flower *Mirabilis jalapa*, commonly known as "four o'clock," has a red and a white flowered variety. If they are crossed the F_1 generation has pink flowers only. But on crossing these among themselves plants in the proportion of one red to two pink to one white flowered are obtained It is obvious that this is an instance of simple Mendelian inheritance, like those already discussed, but that the dominance of red colour is not complete. In spite, however, of the apparent blending of the red and white factors in the F_1 generation, in reality they remain distinct in the germplasm and segregate at the formation of the germ cells as is shown by the F_2 generation.

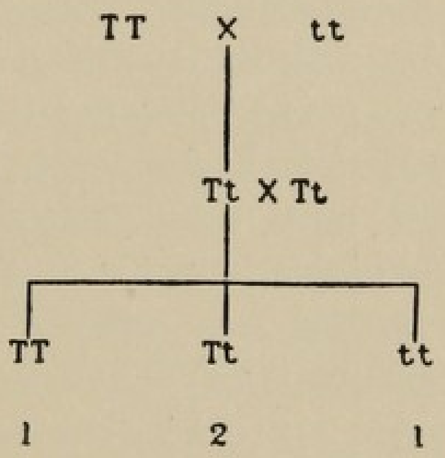


Fig. 8.—Factorial representation of the inheritance of tall and short varieties of sweet pea.

A second case is afforded by the Blue Andalusian fowl. For many years it has been known to breeders that it was impossible to get a strain of these fowls breeding true to type. The reason is now known to be that the Blue Andalusian is a heterozygote, obtained by crossing black and splashed white birds. Hence mating Blue Andalusians always results in a progeny of black, blues and whites in the ratio of 1 : 2 : 1.

Applications of Mendelism.—That the discovery of Mendelian inheritance is not merely of academic interest is abundantly shown by the production of new and important varieties of agricultural plants. Prof. Biffen, by working on these principles, raised a strain of wheat which was immune to the attacks of a fungus causing a disease known as "rust." Also the study of human pedigrees has demonstrated that several diseases follow the simple Mendelian law, e.g. brachydactyly, where the fingers and toes are abnormally short, and feeble-mindedness, which in some forms is recessive to the normal mental condition.

Eye colour in man can also be quoted. Eyes are of many colours. Some have pigment on both sides of the iris, while others have no pigment in front of the iris: to this class belong the blues and grey, while the first class gives rise to the brown, hazel, green, etc. In pink eyes, characteristic of albino animals, the pigment is entirely absent. The inheritance of these various eye colours has recently been shown to be complicated, but, broadly speaking, brown, hazel, green, etc., are dominant to blue. It is evident, therefore, that two blue-eyed people will always have blue-eyed children. Brown-eyed people, on the other hand, may or may not have blue-eyed children, according to their factorial composition.

In the comparatively short period since 1900 it has been shown that Mendelian inheritance is widespread among animals and plants, and applies to a great variety of characters. In illustration the examples on the following page are given :

Dominant.	Recessive.
PLANTS.	
Tall stem (peas).	Short stem.
Round seeds (peas).	Wrinkled seeds.
Yellow seeds (peas).	Green seeds.
Purple flowers (peas).	White flowers.
Yellow cotyledons (peas).	Green cotyledons.
Dentate leaves (nettle).	Slightly dentate leaves.
Short style (primula).	Long style.
Absence of awn (wheat).	Presence of awn.
Susceptibility to " rust " (wheat).	Immunity to " rust."
Hard endosperm (wheat).	Floury endosperm.
Two-rowed ears (barley).	Six-rowed ears.
ANIMALS.	
Coat coloured.	Albino.
Short hair in rabbit and guinea pig.	Long " Angora " hair.
Hornlessness in cattle.	Horned.
Rose and pea combs in fowls.	Single comb.
Normal movement in mice.	Waltzing movement.
Broodiness in fowls.	Absence of broodiness.
Brown pigment in iris of eye in man.	Absence of pigment.
Unbanded shell in wood snail.	Banded shell.

Development of Mendelian Theory.—So far consideration has been given to cases in which the parents differ from each other in only one pair of alternative characters, or " allelomorphs," as they are called. This has been deliberate for the sake of simplicity. In studying inheritance, however, it is general to find that the races of animals and plants differ from one another by several such pairs of characters. It will be well, therefore, to describe what occurs when crosses are made between individuals differing by two pairs of factors. In the list of Mendelian factors just given it is seen that purple flowers in some races of pea are dominant to white ones, and their inheritance is therefore like that of tall and short stems.

If now a tall purple flowered pea is crossed with a short white flowered one, the hybrid offspring are all tall with purple flowers, since both these characters are dominants. But when these offspring plants are crossed together (*inter se*), or with similar ones, products of another experiment of the same character, the resulting F_2 generation will be composed of purple talls, purple shorts, white talls, and white shorts in the proportion of 9 : 3 : 3 : 1. The ratio of purple flowered plants to white or of tall plants to short is the same as in the first experiment described, viz. 3 : 1, for there are twelve talls to four shorts and twelve purple flowered to four white flowered. On the other hand, the crossing of these races differing by two allelomorphic characters results in the production of new combinations. The original parents were purple talls and white shorts, but the second generation contains besides these white talls and purple shorts. How can this be explained on the factorial hypothesis? If P is the factor for purple flowers and p that for white ones, T the factor for tallness and t that for shortness, the parents will have the constitution PTPT and ptpt respectively (Fig. 9). Each of their germ cells will carry the factors PT or pt, so that on fertilization the resulting hybrids will be constituted PTpt. In the production of their germ cells segregation will occur between the factors for purpleness and whiteness and between those for tallness and shortness, and as the two pairs of characters are independent of each other any combination may

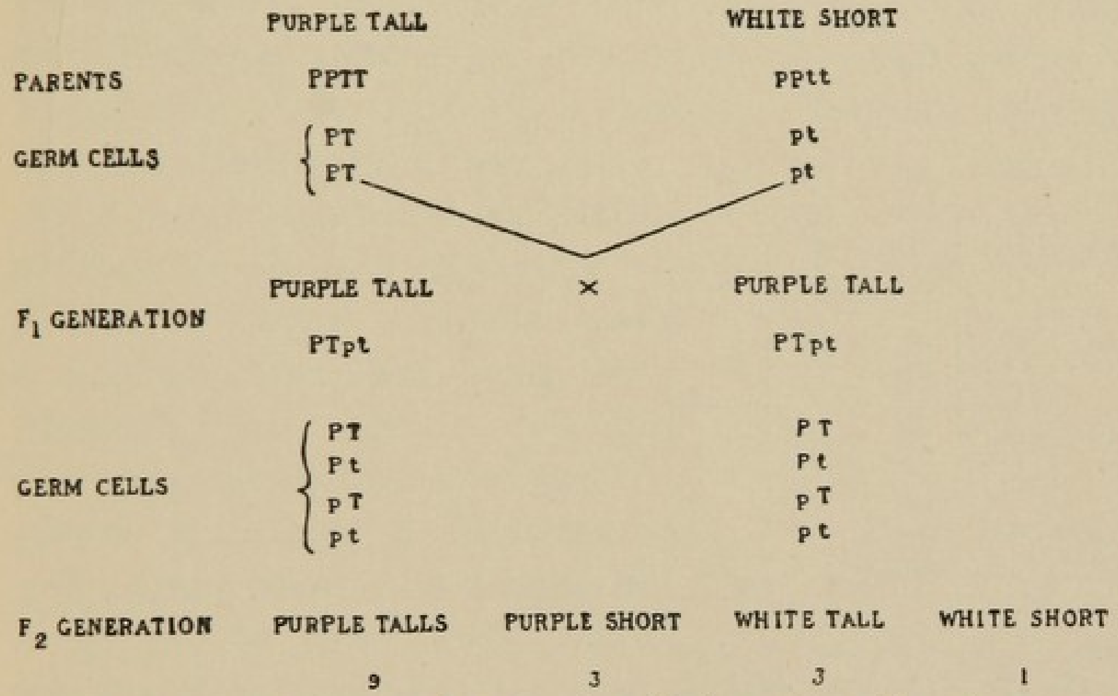


Fig. 9.—Inheritance of two pairs of alternative characters: purple and white coloured flowers, tall and short stems.

take place provided that the factors for the same pair do not associate in the same germ cell. Under these conditions there will be produced in equal numbers four types of germ cells: PT, Pt, pT, pt. At fertilization these can meet one another at random. The problem, therefore, is resolved into finding in how many different ways these four types of germ cells can combine. The answer is 4PpTt, 2PpTT, 2PPTt; 1PPTT; 2Pptt, 1PPtt; 2ppTt, 1ppTT; 1pptt.

Whenever PT occurs the plants will be purple talls, for P and T are dominant to p and t, the first four types of combinations will therefore give nine purple talls ; in the next two P is present but not T, thus giving three purple short ; the next two containing T but not P will result in three white talls, while the last having neither P nor T will be a white short.

Further, of the above types each contains one plant pure in respect of both characters. Therefore by crossing not only have two races been produced, as already pointed out, but a proportionate number of each race is immediately established as breeding true to type.

A simple manner of finding the various ways in which the germ cells can combine is by the "chessboard" method. Where four different types are concerned a square is drawn divided into sixteen parts (Fig. 10). Each term of the germ cells series is written vertically down each of the four sets of squares, and then horizontally across each of the four sets. In this mechanical way all the possible combinations are obtained.

	PT	Pt	pT	pt
PT	PT PT	Pt PT	pT PT	pt PT
Pt	PT Pt	Pt Pt	pT Pt	pt Pt
pT	PT pT	Pt pT	pT pT	pt pT
pt	PT pt	Pt pt	pT pt	pt pt

FIG. 10.—Chessboard method for finding the possible combinations of four differently constituted germ cells.

As Mendel pointed out, his principle of inheritance may be extended almost indefinitely. Parents may differ in respect of three pairs of characters A, B, C dominant to a, b, c. The first generation hybrids will all be of the form ABC ; but the F_2 generation will be in the ratio of 27ABC, 9ABc, 9 AbC, 9aBC, 3Abc, 3aBc, 3abC, and 1abc.

This example serves to demonstrate how extremely complicated the question becomes as the number of alternative pairs increases; and modern breeding experiments show that, in many cases, apparently well-defined characters are represented by a multiplicity of factors. This makes the work very difficult, as the factors have to be sorted out before the explanation of the mode of inheritance of the character can be given.

VI

FURTHER EXAMPLES OF MENDELISM

Inheritance of combs of fowls—Colours of flowers—Reversion—Linkage—Nature of factors.

SO far consideration has been given only to those characters showing a straightforward and relatively simple mode of inheritance. Mendel was fortunate in choosing for his experiments such forms; instead he might easily have decided upon some of the more difficult cases and obtained results which would have given no clue to a law of heredity. For example, had he studied the inheritance of the combs of fowls he would at once have experienced difficulties.

Inheritance of Combs.—Various breeds of fowls are characterized by a certain type of comb, thus that of the Wyandotte is flat and corrugated with a backwardly pointing projection. This is called a rose comb. The pea type comb of the Brahma breed is also flat, but has lateral ridges, while the single type found in Leghorns, Rhode Island Reds and Sussex stands high above the head and is deeply notched along the upper border. Finally, a fourth type, the walnut, occurs in Malay breeds, and is so called because of its resemblance to a half walnut.

Both rose and pea types act as dominant to the single, but when rose and pea are crossed the walnut type appears.

Moreover, when these birds are mated together a

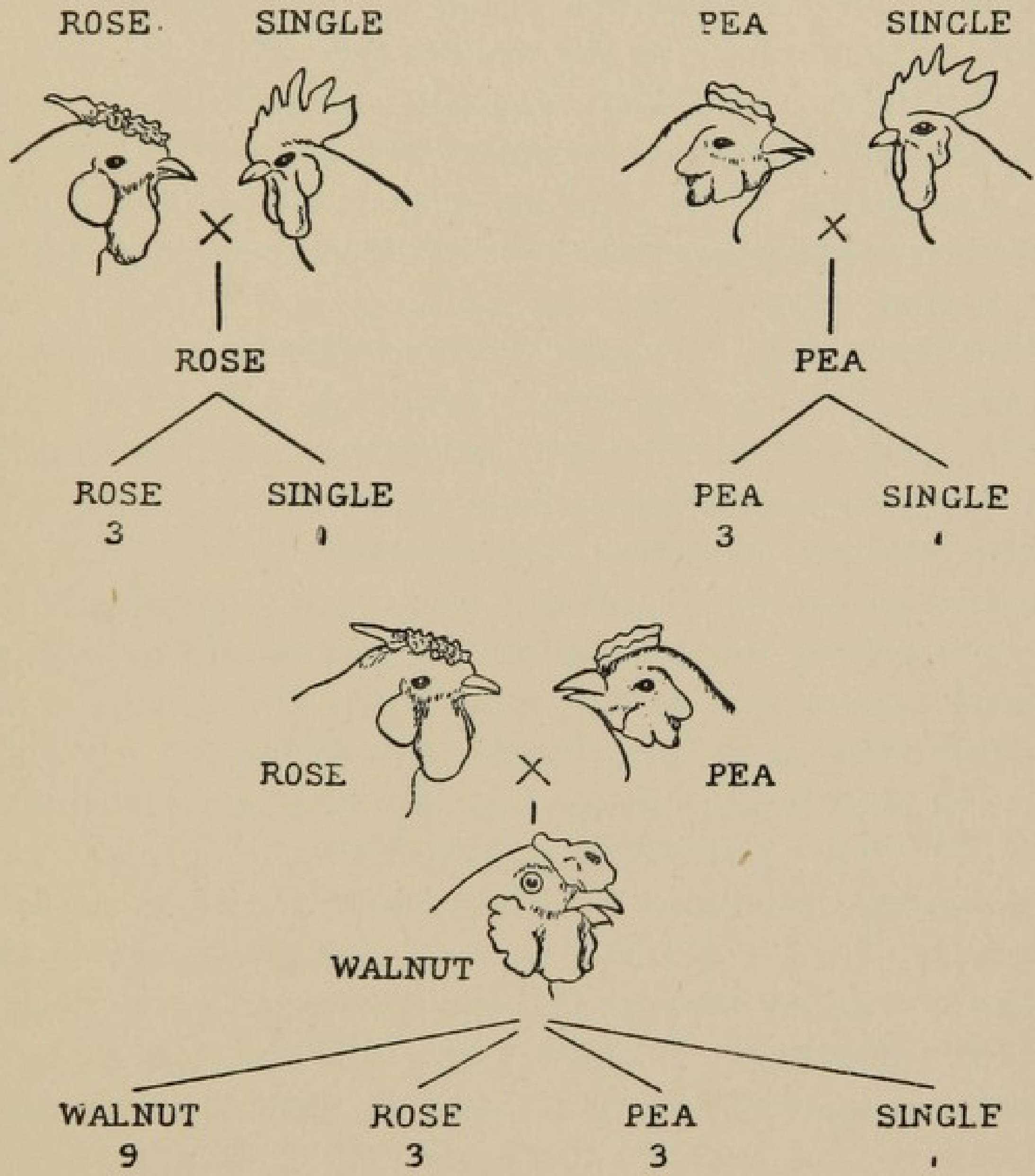


FIG. 11.—Inheritance of comb characters in fowls.

curious result is obtained. As would be expected, walnut, pea and rose types are found, but in addition birds carrying the single comb are produced, in the proportion of nine walnut, three rose, three pea and one single. This ratio at once demonstrated that two pairs of factors are operating, and the result can be explained on the hypothesis that whenever the factors for rose and pea comb are both present their interaction results in the walnut type (Fig. 11).

Inheritance of Colour.—Another interesting example is afforded by certain strains of sweet pea. In general, plants with white flowers give nothing but white flowered offspring: they breed true; crossing white flowered plants produces nothing but whites. But there are races of white flowered plants which when crossed give red flowered offspring. If these reds are self-fertilized the next generation consists of nine red and seven whites. The explanation is that the red colour is due to the interaction of two factors, called by Bateson C and R. One of the original parents contained C, and the other R, but as these factors were not present in the same plant the flowers were white. Crossing, however, brought the factors together and red flowered plants resulted with a constitution CcRr, since Cc and Rr are each alternative pairs. The germ cells produced by these hybrids will be of four kinds, CR, Cr, Rc and cr, and by using the chess-board method described in the last chapter the results of random union of these germ cells are seen to be a ratio of nine plants with C and R, and therefore red; three with c and R, three with C and r and one with c and r, that is seven whites, for R or C alone cannot produce colour.

The white plants, therefore, though in appearance identical, from the point of view of breeding may be divided into three classes. Similar cases, in which individuals, apparently the same, give different breeding results, are comparatively common and make it necessary for the research worker to spend a great deal of time discovering the factorial composition of his material before beginning to make experiments in crossing.

Another interesting feature of this colour inheritance is that the essential bodies for colour production are chemical, one being an organic base, or "chromogen," the other an oxidizing ferment. The details cannot be entered into here, but the principle is important in giving a possible clue to the nature of Mendelian factors.

The production of red flowered sweet peas has been cited because it is one of the simplest cases, involving only two pairs of factors. But research has shown that the various shades of colour and their distribution can also be explained on Mendelian lines by the mutual action of numerous factors. What a few years ago seemed an impossible task, viz. to formulate rules for colour inheritance, is now accomplished, and accurate forecasts can be made as to the result of crossing differently coloured individuals, provided the factorial composition is known.

Reversion.—It is widely held, and with a certain amount of justification, that hybrids between two strains of the same species tend to revert to the ancestral type.

This is probably due to the re-assemblage of the original factors, which have been separated from one another during the evolution of the various strains from their common ancestor.

A famous case of reversion is the occasional appearance of hybrid pigeons resembling the wild blue rock.

Darwin made use of this as an argument for the origin of domesticated varieties of animals and plants from a wild species. Staples-Brown has shown that this case of reversion can be explained in Mendelian terms. Crosses made between black barbs and white fantails give all black birds splashed with white. On breeding these together the second generation consists of blacks (with and without white splashes), blues (with and without white splashes) and whites in the ratio of 9 : 3 : 4. There are two pairs of factors concerned, one for colour C, the other a modifier B, in the absence of which the colour of the birds is blue. The original black barbs contained both factors, CCBB, but the white fantail contained neither, ccbb. The first generation birds would, therefore, have the constitution CcBb, giving germ cells of four sorts, CB, Cb, cB, cb. The result of bringing these germ cells together can be found in the manner already explained, and it will be seen that the blue birds are of constitution CCbb or Ccbb, that is they lack the modifying factor B for turning the colour from blue to black.

So far only the interaction of factors in producing colour changes have been discussed, but cases are known where colour and structural factors are connected. For example, in stocks, crosses between a smooth-leaved cream flowered variety and a smooth white, give purple flowered hoary plants ; which are similar to the ancestral type. The origin of the purple colour is the same as in the sweet peas just described ; one factor for colour has been introduced by one parent and the other factor by the other. The hoariness is, however, different ; it appears because its factor can only take effect when in the presence of purple colour. The parents, therefore, were smooth-leaved, although carrying the hoary factor, because the right conditions for purple colour were not present. The F_2 generation is composed of purple, white and cream flowered plants in the usual proportion, but only the purple are hoary.

Linkage.—So far the separate pairs of factors have been treated as segregating independently, but, as was first shown by Bateson and Punnett in 1906, this does not always occur.

There are two strains of sweet pea, known as the "Duke of Westminster" and the "Painted Lady," characterized by having in the first case purple coloured flowers with hooded standards, and in the second red flowers with erect standards. Purple is dominant to red and erect to hooded.

Crosses between the two give, as expected, erect standard purple flowers, of the "Purple Invincibles" type, but the F_2 generation contains the three types in the ratio of one Duke of Westminster, two Purple Invincibles, one Erect Red.

It is at once striking that there are no hooded reds among the progeny and that the ratio is 1 : 2 : 1 (characteristic of one pair of factors) instead of 9 : 3 : 3 : 1. But this is at once explained if it is assumed that the factors for shape of the standard and colour of the flower do not segregate at the formation of the germ cells, but are distributed as though they were one factor.

Thus on the factorial scheme the purple coloured, hooded standard variety would have a constitution PPee (since purple is dominant to red and erect to hooded), the red flowered erect standard variety ppEE ; and the hybrid purple flowered erect standard plants would therefore be PepE.

If there were no linkage four types of germ cells would be formed, Pe, PE, pE, pe ; but since the factors for colour and shape of standard stick together the germ cells are of only two kinds, Pe and pE, which by random combination give the required ratio in the F_2 generation.

Such association is known as " linkage."

In *Drosophila melanogaster*, a small fruit fly which has served as material for the researches of Prof. Morgan and his collaborators in the United States, linkage has been studied more extensively than in any other animal or plant. The wild fly has long wings and a grey body, but during the experiments flies with differently coloured bodies and shaped wings have appeared, one, for instance, having a black body and short vestigial wings, both of which characters are recessive to the normal condition.

Crosses between a black fly with vestigial wings and a wild (grey long wing) fly give only grey with long wings. When such a male is mated back to one of the black vestigial winged females, the offspring are 50 per cent. grey with long wings and 50 per cent. black with vestigial wings (Fig. 12). It is clear that the factors for grey colour and long wing are linked together and have no tendency to separate during the formation of the germ cells. Grey colour and long wing or black colour and vestigial wing went into the cross together and they came out together.

In these two cases the linkage was complete, but in the reciprocal cross to the above, i.e. mating a grey long female with a black vestigial male, instead of obtaining 50 per cent. grey long and 50 per cent. black vestigial as before, there was produced 41·5 per cent. grey long, 41·5 per cent. black vestigial, 8·5 per cent. black long and 8·5 per cent. grey vestigial. That is to say in 17 per cent. of the cross the linkage between grey and long, black and vestigial had broken down. By choosing other examples a series could be given ranging from complete linkage to conditions where its extent is

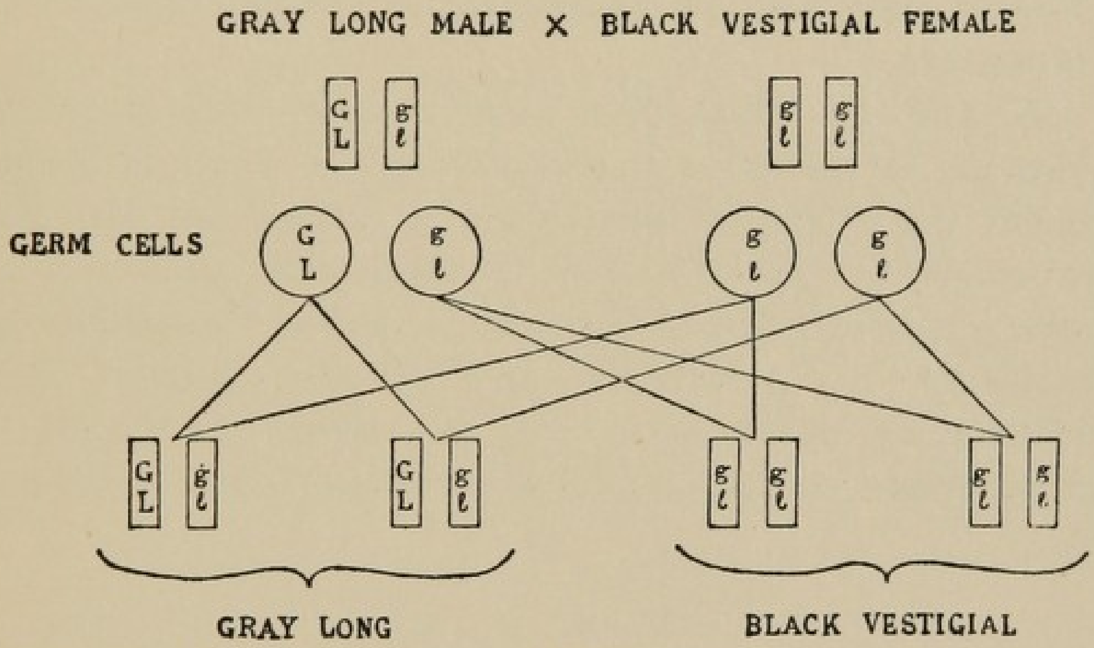


FIG. 12.—Linked inheritance of the characters grey body, long wing and black body, vestigial wing in Drosophila.

slight. Here it is sufficient to describe the occurrence and consider it further in a subsequent chapter.

Nature of Factors.—Throughout we have used the familiar expression "factor," but there is a danger in this, since there is a tendency to form a picture in one's mind of the factor as being a miniature replica of the character in question.

Of course nothing can be further from the truth. As is shown later, the heritable characters are probably carried by certain elements of the cell nucleus which are known as chromosomes. The substance composing these chromosomes has at certain definite places a characteristic constitution, and it is due to this characteristic constitution that a certain character arises in the adult organism. How this occurs is at present unknown, but it must be clearly recognized that when the word " factor " is used in connection with Mendelism it is not intended to convey the idea of a definite structure or configuration of the character it represents.

Within the limits of a book such as this it is not possible to do more than indicate the kind of result which the study of Mendelism is giving, but the few experiments described are, nevertheless, sufficient to give a general idea of the way in which these distinct variations are inherited, and to demonstrate how widespread is the law, both as regards the species of animals and plants, and the type of characters following it.

VII

CYTOLOGY AND MENDELISM

Cells, division of cells—Formation of germ cells—Linkage —Crossing over.

IN the last two chapters it has been shown that the factorial hypothesis of heredity explains the results of breeding experiments ; and because of this ability it may be accepted as a true one. The material basis of Mendelian inheritance can then be conceived as consisting of separate units maintaining their individuality throughout the life of the animal or plant. The fertilized egg contains a double set, for it has been formed by the union of a maternal and of a paternal germ cell ; but when the individual, arising from this egg, in its turn forms germ cells, the units segregate one from another.

It is now known that in the germ cells there are living structures which behave in such a way as to satisfy these conditions. It will be convenient, therefore, to give, for those who are not students of natural history, an account of how plants and animals multiply—in fact of the genesis of new individuals and the sequence of generation.

Cells.—Cells form the bodies of all living organisms. One group of animals and plants are single cells (the bacteria and the protozoa) ; but in the majority of cases each individual is composed of thousands of these small bodies, all of which have originated from one single fertilized egg, by its division first into two, then into four and so on until a great mass is formed. Certain cells then are specialized for particular functions, and become bone cells, muscle cells, nerve cells, skin cells, etc.

Difficulty is sometimes found in understanding exactly what is meant by a cell; perhaps the reason why these bodies were given the name may make it clear. At the end of the seventeenth century the then secretary of the Royal Society, Dr. Robert Hook, published a book entitled "Micrographia." In it were figured various natural history specimens as seen under the microscope and among them a piece of cork. This was shown to be composed of numerous empty little chambers resembling boxes, in size less than 1/100 inch; and because of their resemblance to the honeycomb of the bee he called them cells. Later it was shown that this cellular structure was characteristic of animals and plants. Also it was found that the cells were not empty, as described by Hook, but were filled with liquid matter, and in 1836 Schwann showed that the important thing about the cell was not the box or the cell wall, but the contents. Nevertheless the term cell, originally used to designate the wall, was retained for the contents, now called protoplasm.

Cells vary much in size, usually measuring from 1/5000th to 1/200th of an inch in breadth, and may be of almost any shape; thus in one tissue they may be arranged as in a honeycomb, in another they may form a close network; they may be elongated and contractile, or again embedded in a hard substance formed around them, as in cartilage and bone.

The protoplasm, forming the living contents of the cell, is slimy, almost liquid, but at the same time tenacious. Seen under the microscope it is semi-transparent and filled with minute granules, so that it resembles an emulsion. It may contain various bodies such as oil drops, large, coarse granules, etc. ; but apart from these it always possesses a special structure, usually spherical in shape, and of a firm

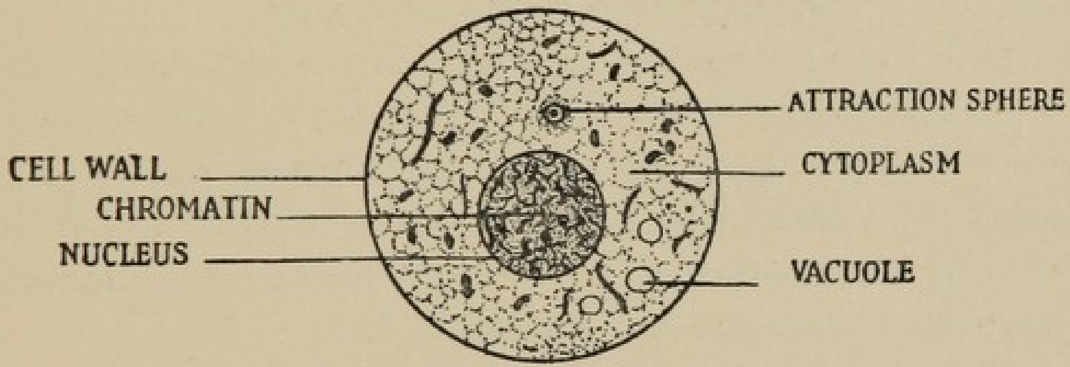


Fig. 13.—Generalized figure of an animal cell.

dense nature, surrounded by a skin. This is the nucleus, which is of vital importance in the chemical changes going on in the cell and in inheritance. The material composing the nucleus, called chromatin, is a complex substance coloured very deeply by carmine and logwood dyes (Fig. 13).

Division of Cells.—When a cell divides into two, curious changes take place in the nucleus, diagrammatically represented in Fig. 14. It must be understood that the details of the process vary somewhat in different animals and plants, but the essentials are the same whatever cell be chosen for study.

Fig. 14a shows the cell prior to division, the chromatin is in the form of minute granules and filaments. Outside the nucleus there is a small body, known as the centrosome, whose division in the animal cells (Fig. 14b) initiates the general process. The chromatin next becomes arranged into a thread (c), which ultimately breaks up into a number of small bodies called chromosomes (d). Their number is the same for the cells of any one species of animal or plant, but may be different in allied species, some having twelve, others eight, and so on. Certain worms have only two ; in the figures four are drawn.

After the centrosome has divided round each half a star-like figure is formed. Separation of these two bodies occurs, and between them there develops a spindle of thread-like strands in the middle of which the four chromosomes become arranged, the nuclear membrane having disappeared (e, f).

Each chromosome now splits along its length (g), and the halves gradually separate and travel along the spindle towards the centrosomes (h).

From now onwards the course of events is the reverse of that which gave rise to the chromosomes ; they lose their individuality and become merged together to form two new nuclei, round each of which a new membrane develops. The spindle also disappears. At the same time the cell becomes nipped into two halves (i, j), with the result that two new daughter cells are produced, each like the one from which they have arisen (k).

This complicated process, known as karyokinesis, seems to have as its main purpose the accurate division of the contents of the mother nucleus into the daughter nuclei. The original number of chromosomes was

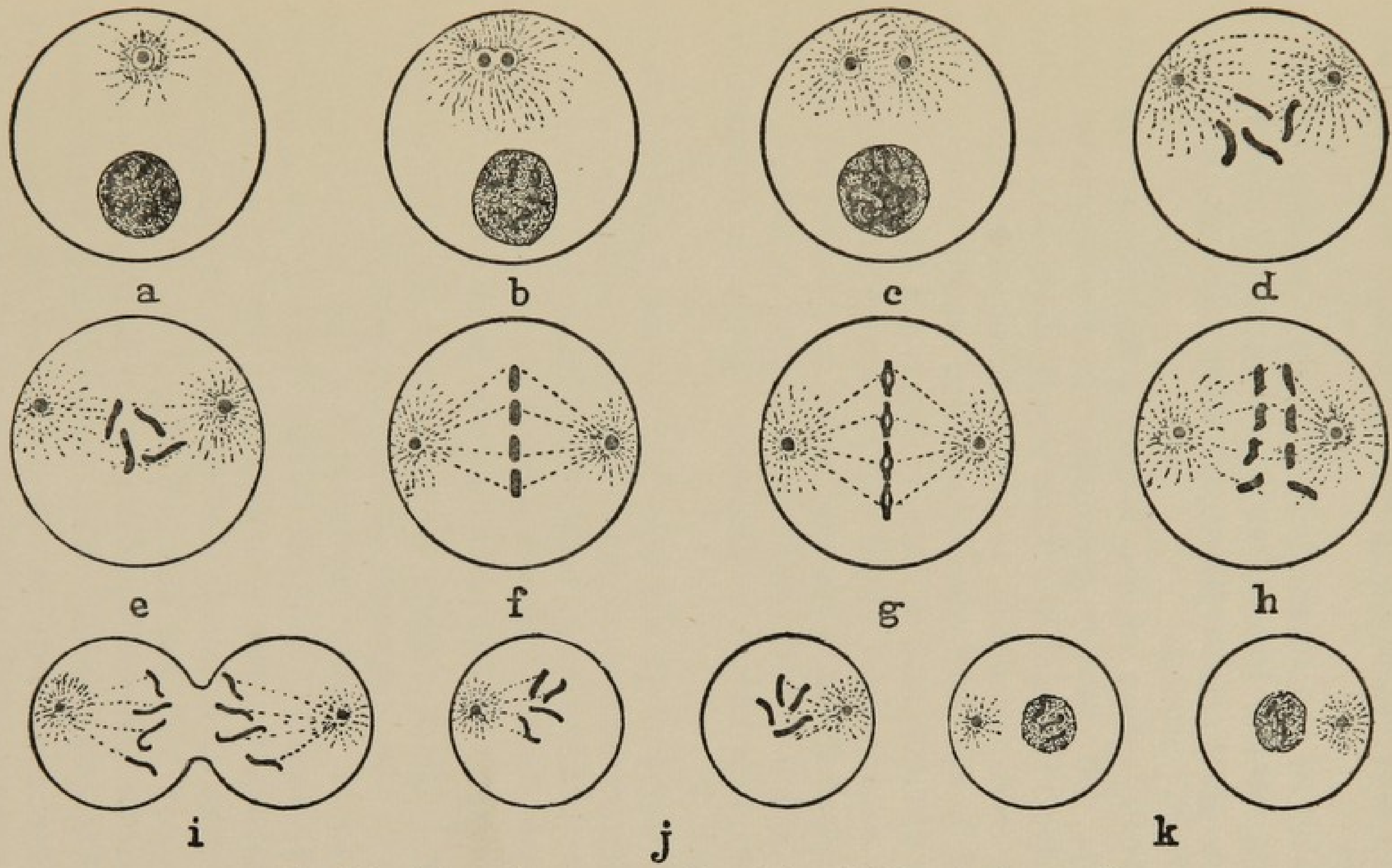


FIG. 14.—Schematic representation of the division of a body cell.

four, and the same number is passed on to the new cells.

This is the method of division obtaining for body cells, that is those forming the various tissues, etc. The germ cells, however, pass through a slightly different process.

Fertilization of the female germ cell by the male germ cell consists essentially in the fusion of their nuclear chromatin. This would produce a fertilized egg with twice the normal number of chromosomes, and in the next generation there would be four times the number, and so on. If this is not to occur (and it has already been stated that the chromosome number is constant for each species), some mechanism is required by which the chromosome number is halved in the germ cells before fertilization. Such an arrangement exists.

Diagrammatically it is easy to show what it is, but it must be recognized that the actual process is complex, and that the germ cells of the male and those of the female do not follow exactly the same course. Here, however, only the essentials can be given.

Formation of Germ Cells.—The nuclear changes leading to the formation of the chromosomes are similar to those already described for the body cells; the chromosomes, however (again four is taken as the number), instead of splitting apply themselves side by side, and in such close union that there appears to be only half the number (Fig. 15). The pairs next separate and pass to each pole of the cell, which divides to form two (c, d). Thus each new cell contains only half the number of chromosomes (e). These cells now divide in the usual way, so that from every original cell there are formed four, each having half the number of chromosomes (f).

As fertilization consists in the union of male and female germ cells the chromosomes of the fertilized egg are derived half from the mother and half from the

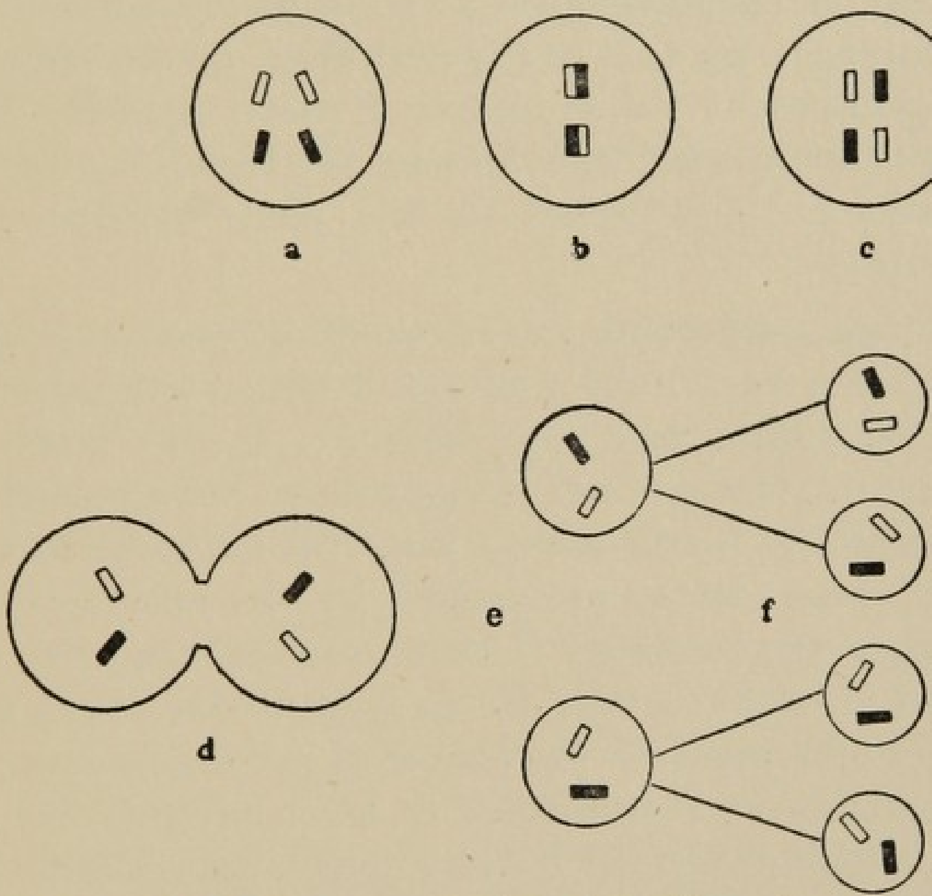


FIG. 15.—Schematic representation of the formation of germ cells, the small rectangles being the chromosomes.

father. Further, and this is of importance, there is evidence that when the chromosomes pair, as just described, the union is between paternal and maternal chromosomes. In Fig. 15 the latter are shown black.

It will be clear to those who have followed this account that the behaviour of the chromosomes is exactly such as is required to explain the behaviour of Mendelian factors, for during the formation of the germ cells segregation of the paternal and maternal components of each pair of chromosomes takes place. Referring once more to the result of crossing purple tall sweet peas with white short ones (Fig. 9), and supposing that the factors for colour are carried by the one pair of chromosomes, and the factors for height by the other pair, it is obvious that, as the pairs of chromosomes at the reductive division separate from one another in a random manner, the Mendelian factors will also be distributed in the same random way (Fig. 16).

Linkage.—Research has shown that each animal or plant has a very large number of characters inherited in a Mendelian way; for instance, in the fruit fly, Drosophila, Morgan and his associates have traced the transmission of well over a hundred different factors. But if these factors are carried by the chromosomes, and since the numbers of chromosomes are relatively few (in Drosophila only four), it is obvious that each chromosome must be the bearer of several factors. If this conclusion is admitted it also follows that the several factors carried by any particular chromosome must necessarily behave as though they were single ones; in other words, in a crossing experiment they would enter as a group and segregate as a group in the F_2 generation.

This is, of course, exactly what does occur in the phenomenon of complete linkage as described in the last chapter.

If in the example given of the linkage between the pairs of factors for body colour and wing structure, grey be called G, and its allelomorph black g, long wings L, and short wings l, and if G and L are considered to be contained in one of the chromosomes, g and l in its companion, then Fig. 12 gives graphically the scheme of inheritance. The rectangles represent the chromosomes bearing the factors of the adult fly, and the circles the segregated chromosomes of the germ cells. In this way an explanation is given for the sticking together of the two pairs of factors.

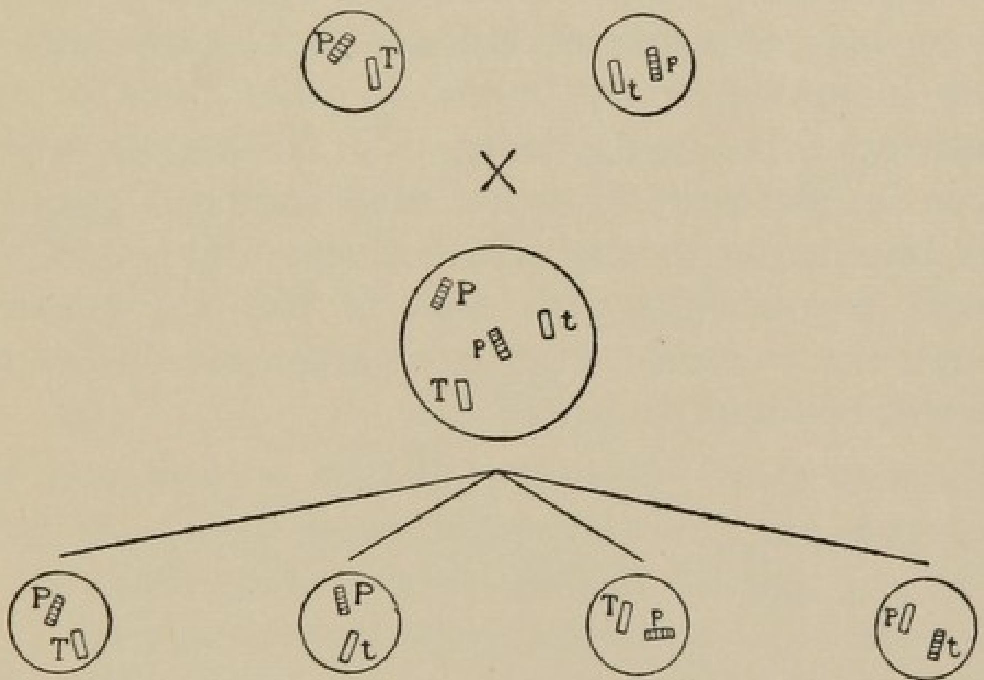


FIG. 16.—Figure showing how the segregation of Mendelian factors can be explained on the assumption that they are carried by the chromosomes.

In Drosophila linkage has been studied very intensively, and it has been found that the linked factors fall into groups. The members of a group A, B, C, D show linkage among one another, but not with those of another group, L, M, N, O, which in its turn is independent of a third group, P, Q, R, S, and so on. The number of these groups in Drosophila is four, which corresponds exactly with the number of chromosomes of the germ cells, thus affording another proof for the view that Mendelian factors are contained in the chromosomes.

In plants linkage groups are known in the sweet pea and the edible pea, and in the primrose and the snapdragon, where there is a group of five linked characters, and in the stocks, where there is one of four; other cases also occur in tomatoes, wheat, maize and oats. But a point of significance is that the records of cases of linkage groups are steadily being increased as the mode of inheritance of more characters is becoming known. Until they are worked out to the same extent as has been done in Drosophila, it is impossible to say whether the number of such groups corresponds with that of the chromosomes, though the evidence all points to the conclusion that this will be found to be the case.

Crossing Over.—Complete linkage is, however, relatively rare; it is much more common for it to be shown in only a partial degree, as was illustrated by the reciprocal cross of the first experiment on p. 82.

Here it was found that in 17 per cent. of the cases the linked groups dissociated one from another. On the hypothesis that the factors are contained in the chromosomes the result can only be explained by assuming that at the reductive division, during the development of the germ cells, there is an exchange of factors between homologous chromosomes. This is known as crossing over. There is good evidence that an interchange of parts of chromosomes does occur, for when the pairs lie close together, just previous to the reduction in number, they become elongated and twist round each other so as to resemble a skein. When the time comes for them to separate, instead of untwisting, a longitudinal split takes place, with the result that certain parts of each chromosome become attached to its fellow.

Fig. 17 will make this clear. Here it has been assumed that one chromosome contains factors G and L and the other one the factor for g, l; as a result of the "crossing over" the factors for L and l have changed places. To avoid confusion a hypothetical case has been taken where the twisting is of the

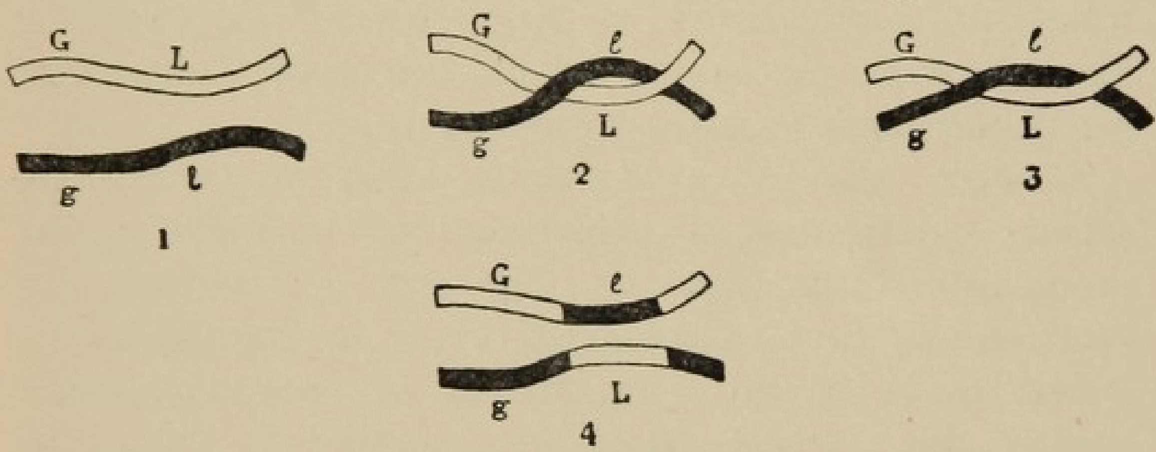


Fig. 17.—Diagram illustrating the possible method by which "crossing over" takes place, owing to the twisting of chromosomes. The factors for grey body, long wing; and black body, vestigial wing, are supposed to be located in the chromosomes at the points indicated by the letters G, L, g, l.

simplest type, but in reality it is usually very much more elaborate, with the result that the crossing over is complicated.

The degree of crossing over of linked characters has been studied in Drosophila, and it is found that the frequency is constant for any particular set of characters. The study of these frequencies has led to most interesting conclusions, for it has been found possible not only to say in which particular chromosome certain factors reside, but further to map out their distribution in that chromosome. Since the chromosomes are exceedingly small bodies, only visible under the highest powers of the microscope, such an achievement is to say the least remarkable.

The evidence for the transmission of inherited characters by the chromosomes is so strong that there is a tendency to assume that the cytoplasm of the cell, that is the protoplasm in which the nucleus lies, is of little or no importance. Such a conclusion is not justified, for it has been shown that the early division stages of development of the fertilized egg and the physiological reaction by which the embryo develops are determined by the cytoplasm.

Another kind of cytoplasmic influence is by the direct transference of substances or structures in the cytoplasm. For instance, the egg of certain sea urchins contain a red pigment which is directly transferred to the embryo. In plants also there are certain bodies, the plastids, which are resident in the cytoplasm and are carriers of inherited qualities, such as the green and white patches in the leaves of *Mirabilis jalapa albomaculata.* These are transmitted by the cytoplasm.

But apart from such direct cases it is obvious that the Mendelian factors carried by the chromosomes can only cause the character to appear by acting on the cytoplasm ; and if the chromosomes can modify the cytoplasm it is reasonable to suppose that the reverse action may take place.

At present this possibility has hardly been tested, but it is a field of research well worth studying, and may give a clue to some of the curious pathological inheritances to which recent writers have given much prominence.

VIII

INHERITANCE OF SEX

Sex chromosomes—Sex-linked inheritance—Sex in plants —Lethal factors.

CONSIDERATION must now be given to one of the most interesting and at the same time elusive of biological problems—that is the heredity of sex. Thirty years ago opinion was dominated by the view that the determination as to which of the two sexes an organism should become was largely a question of the influence of the surroundings during development. To-day, on the other hand, the evidence is conclusive that the sex is already determined in the fertilized egg, and has its basis in certain peculiarities of the chromosomes. The behaviour of the chromosomes during the reduction divisions shows that in the body cells they should be found in even numbers, for the possibility of being reduced by pairing demands an even number. About twenty-five years ago, however, the extraordinary discovery was made that in the cells of certain insects there was an odd number of chromosomes. It is now known that where this occurs it is usually in the male sex, and that then the number is often one less than in the female. Thus if the latter has six chromosomes in the body cells, the former has only five. An irregularity is, therefore, introduced into the pairing of the chromosomes during the formation of the germ cells. In the male, during the reduction stage, all the chromosomes pair except one, which has no mate. This, the X chromosome as it is called, passes into one of the daughter cells. At the next division every chromosome divides into two, the products of the division passing into the germ cells so produced. Thus there are formed two kinds of male

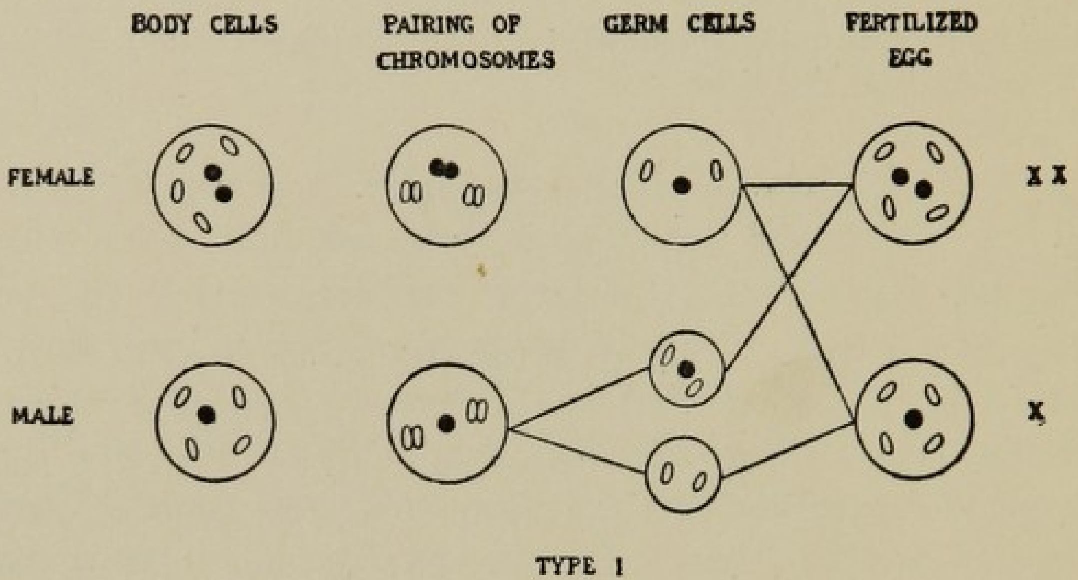


FIG. 18.—Scheme showing the distribution of the sex chromosomes at the formation of the germ cells in animals, the male of which has one less than the female. The sex chromosomes are shown in black, the other chromosomes white.

germ cells in equal numbers, one kind containing the X chromosome, the other kind lacking it (Fig. 18). The first type has three chromosomes and the second only two. In the female, on the other hand, the mate to the odd chromosome of the male is present; she possesses XX chromosomes. Therefore, during the formation of the egg the chromosomes pair and the resulting cells all have an X chromosome (Fig. 18). The chromosome number is therefore three.

Sex Chromosomes.—It is evident that at fertilization the egg may be fertilized by a germ cell carrying an X chromosome, or by one lacking it. In the first case the fertilized egg will possess six chromosomes, and in the second case five. And since females are characterized by having six chromosomes and males by having five, it is evident that a sperm with an X chromosome is a female determiner, whilst one without it is a male determiner.

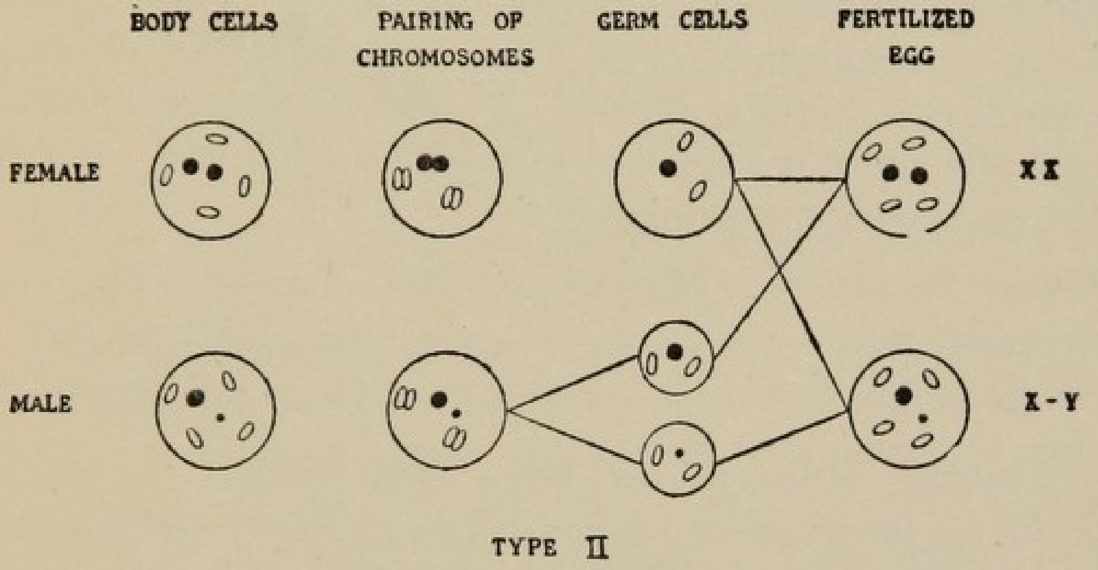


FIG. 19.—Scheme showing the distribution of the sex chromosomes at the formation of the germ cells in animals, where in the male they are of unequal size. The sex chromosomes are shown in black, the other chromosomes in white.

Shortly the system may be presented as follows :

Female Germ Cell.		Male Germ Cell.		Fertilized Egg.
(n + X)	+	n	=	2n + X (male)
(n + X)	+	(n + X)	=	2n + 2X (female)

where n = the number of ordinary chromosomes characteristic of the species.

An objection to this view of sex determination was that it was not universally found that the chromosome number in the male was less than in the female. The difficulty has been removed, however, by the discovery that in many species of animals, though both sexes possess the same number of chromosomes, in the male there is a pair of unequal sized sex chromosomes, which separate from each other at the reduction division. Here, as before, two classes of sperms are produced, one having a large chromosome and the other a small one. The female, having an equal pair of large chromosomes, produces eggs all of which have a large chromosome (Fig. 19). The unequal chromosomes are usually termed X and Y chromosomes; and the male is said to have an X — Y pair. Using the same scheme as above :

Female Germ Cell.		Male Germ Cells.		Fertilized Egg.
(n + X)	+	(n + Y)	=	2n + XY (male)
(n + X)	+	(n + X)	=	2n + 2X (female).

Further observations have shown that a whole series of forms occur, ranging from those in which the Y chromosome is absent, through those in which it is small, reaching a final condition in which it is of practically the same size as the X chromosome.

The condition where the male has only one X chromosome has now been described for many groups of animals. In addition to a number of species of Insects it is known to occur in some spiders, in a number of parasitic worms and in several Mammals, including Man ; and the other types of sex chromosomes are also widely distributed.

It must not be supposed that this simple explanation of sex determination is the complete one ; as our knowledge increases it becomes more and more evident that this basic property of life is bound up with many different agencies, but the chromosome differences are certainly of fundamental importance. Various conditions may alter their action; they may themselves vary in power or be affected by external conditions, with the result that abnormal individuals, intermediate between male and female, may appear. Also it has been found that in vertebrates the sex chromosomes cease to act after the formation of the sex glands, which, by pouring into the body a secretion, continue the task of sex determination. Because of this, removal of the reproductive tissue in such animals exerts a profound influence. In Insects, on the other hand, the chromosomes appear to dominate throughout life, and removal of the sex glands produces no effect.

Parthenogenesis, where young are produced without the co-operation of the male, and hermaphroditism, where male and female organs are found in the same animal or plant, are aspects of the sex problem, of which there is scanty knowledge. What little there is, however, points to the conclusion that the sex chromosomes are of importance.

Sex Linked Inheritance.—If chromosomes are the bearers of Mendelian factors, and this has been shown to be the case, the expectation would be that the sex chromosomes also contain factors which would be distributed in the same manner as are the sexes. Such an expectation has been established, and the coupling of characters with sex distribution has been termed "sex-linked inheritance."

As an example, the eye colour of the fly Drosophila may be quoted. In the normal (wild) insect the eye is red, but in a brood of these flies there suddenly appeared by mutation a male with white eyes. If such white-eyed males are bred with red-eyed females, the resulting generation are all red-eyed and of both sexes.

On pairing two of these together, however, there are produced red-eyed males, white-eyed males and red-eyed females, but no white-eyed females.

Again, when a white-eyed male is paired with a heterozygous red-eyed female (one impure for red), the offspring show all possible combinations, i.e. red and white males and red and white females.

Finally, if a red-eyed male is crossed with a white-eyed female, the resulting generation contains half white-eyed males and half red-eyed females, thus all the males are white-eyed.

The results may be summarized thus: If R represents the factor for red eye, r that for white eye, then:

(1) Red female × white male — Red males, red females.
RR rr = Rr Rr

(2) F_1 red female × red male — Red males, white males, red females of two kinds.
Rr Rr = Rr rr Rr and RR

(3) F_1 red female × white male — Red males, white males, red females, white females.
Rr rr = Rr rr Rr rr

(4) White female × red male — White males, red females.
rr Rr = rr Rr

Such a scheme of inheritance appears to be somewhat complicated, and until the significance of the sex chromosomes was realized it was difficult to understand the apparent discrepancies in the distribution of the characters with the sexes. When, however, the assumption is made, and there is abundant evidence to justify it, that the white-eyed character is carried

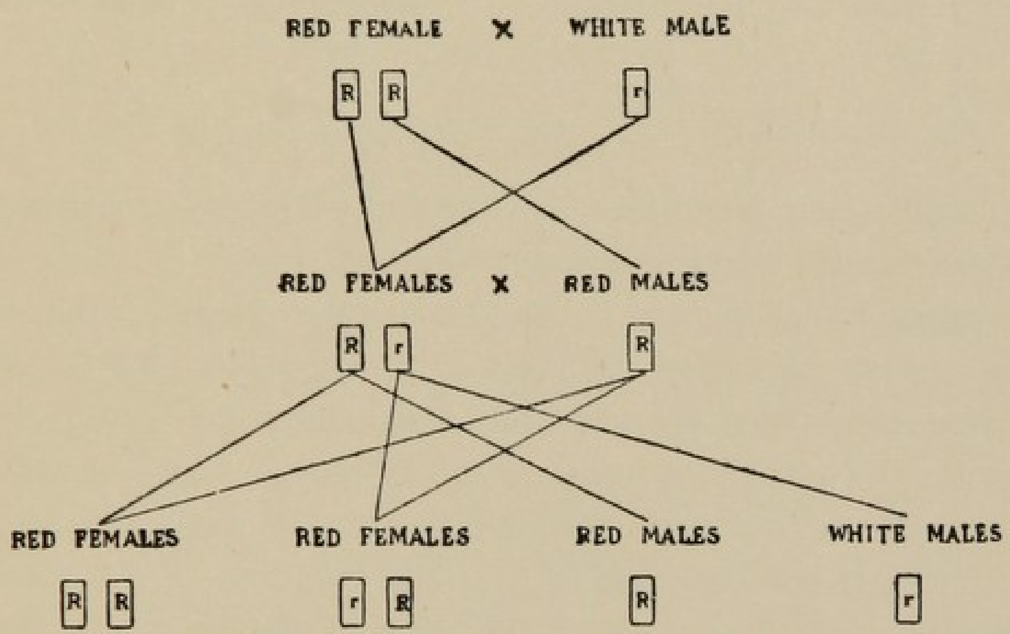


FIG. 20.—Inheritance of a sex linked character in Drosophila on the assumption that the factor is carried by the X chromosome of the male. The sex chromosomes are represented as rectangles and as they only are shown, two rectangles correspond to a female, one to a male.

by the sex chromosome of the male, the difficulties disappear.

In Drosophila the sex chromosomes are of the X — Y type, but as the Y component carries no factor connected with eye colour it has been omitted from Figs. 20, 21, 22.

These show diagramatically the mating given in the scheme above, the first two being grouped together in Fig. 20. As the rectangles represent the sex chromosomes, when there are two the insect is a female, but when only one is present a male is produced. And as

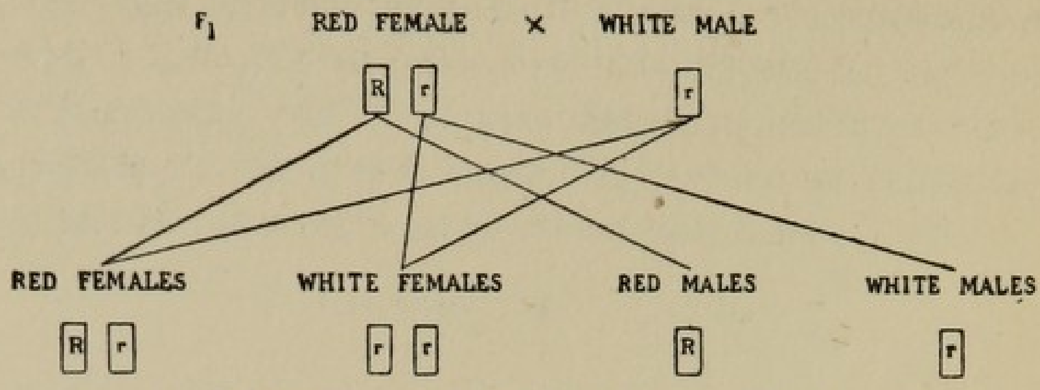


Fig. 21.—Inheritance of a sex linked character as in Fig. 17.

R is dominant to r, the F_1 females of Fig. 17, although of the constitution Rr, are red-eyed.

Similar cases of sex linkage are known in Man ; the commonest of these is colour blindness. As is well known, this condition is fairly frequent in males, but relatively rare in women. A defective man married to a normal woman has only normal children (Fig. 23), though the daughters, having the factor for colour blindness (n), are capable of transmitting it to their sons. If, therefore, one of these transmitting women marries a normal male some of their sons will be defective and some normal. All the daughters will appear to be normal, but half of them will be transmitters of the defect.

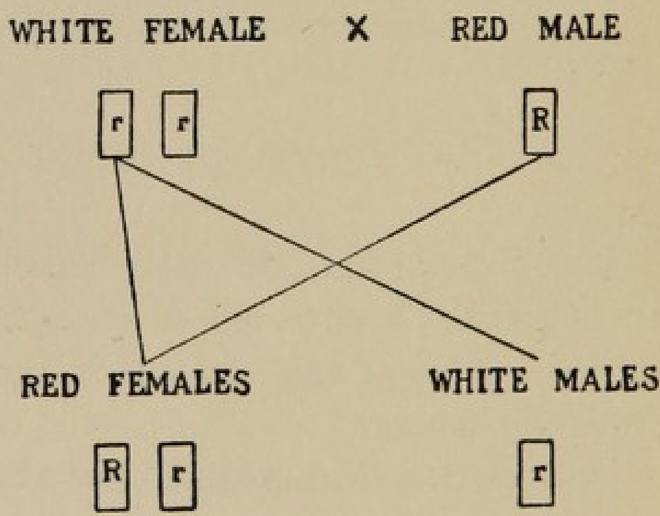


Fig. 22.—Inheritance of a sex linked character as in Fig. 17.

Crossing over in sex linked characters is also known to occur, but it has been observed in the female only. If a female Drosophila with yellow wings and white eyes is mated to a male with grey wings and red eyes,

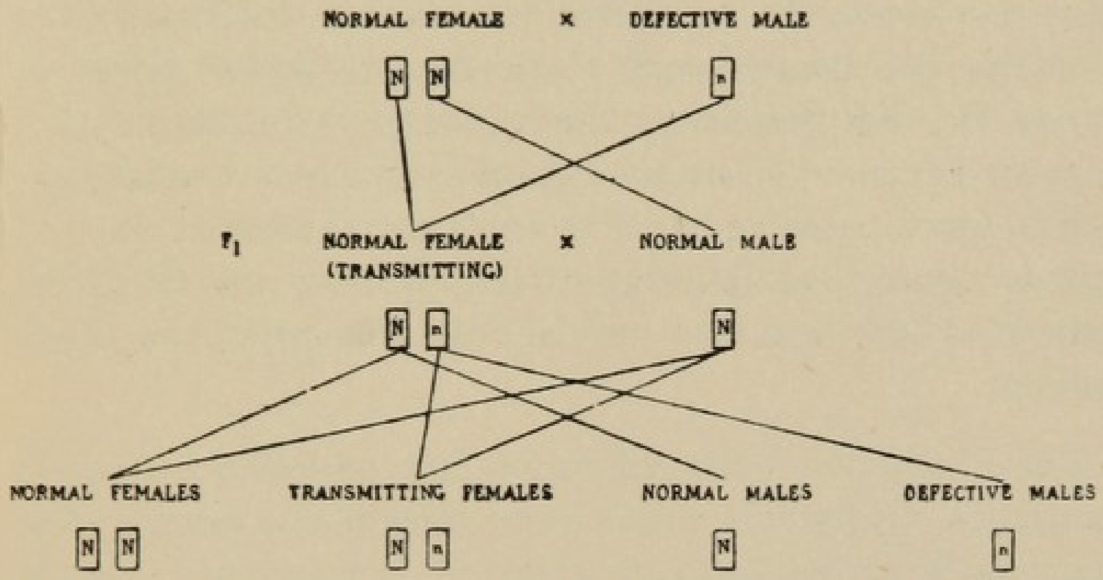


FIG. 23.—Inheritance of the sex linked character colour blindness in man. The scheme is on the same principle as that of Fig. 17.

the sons are yellow and white and the daughters grey and red. On breeding these together a small amount of crossing over takes place, with the result that the offspring are in the following ratios:

Yellow white, grey red.	Yellow red, grey white.
99%	1%

On the assumption that the factors for yellow and white are carried by the X chromosome the scheme of inheritance can be worked out in the same manner as for red and white eyes.

Sex Linked Inheritance in Birds and Lepidoptera.—Breeding experiments have shown that in Lepidoptera (Butterflies and Moths) and Birds, the sex linked inheritance is exactly the reverse of that found in Drosophila and Man. The female and not the male is heterozygous for the sex-linked factors; and, therefore, produces two kinds of germ cells. It is of great importance and interest to find that cytological evidence leads to the same conclusion, for in certain moths it has been shown that the number of chromosomes in the female is one less than in the male; exactly the reverse of the condition in other animals.

For the birds no complete demonstration of this is at present available, though investigations on the fowl indicate that they also will fall into line with the other results.

Sex in Plants.—No reference has as yet been made to plants, though it must have struck the reader that sex is as well developed in them as in animals. And it must be confessed that the plant has proved a stumbling block to the acceptance of sex-determination on the chromosome hypothesis; for until very recently no evidence of sex chromosomes could be obtained.

By the nature of the case the plant is not so favourable as the animal for such a study, for the majority of higher forms are hermaphrodite. But evidence is now brought forward showing that in several diœcious species sex chromosomes are present, and that in one of them (*Lychnis dioica*) there is a sex-linked character for narrow leaves.

Further discussion would be premature, but the results are important in indicating that the method of sex-determination is in essentials the same in both animal and plant kingdoms.

Lethal Factors.—Before ending the chapter brief reference must be made to an important extension of the Mendelian theory. The hypothesis of sex-determination already outlined would result in the production of males and females in equal numbers. This is, of course, provided that no external agencies can modify the action. As a matter of fact several are known. But apart from these there are inherited factors, known as "lethals," affecting the sex ratio.

These factors are in no way different from those giving rise to structural changes or colour variations : they are simply local changes in parts of the material

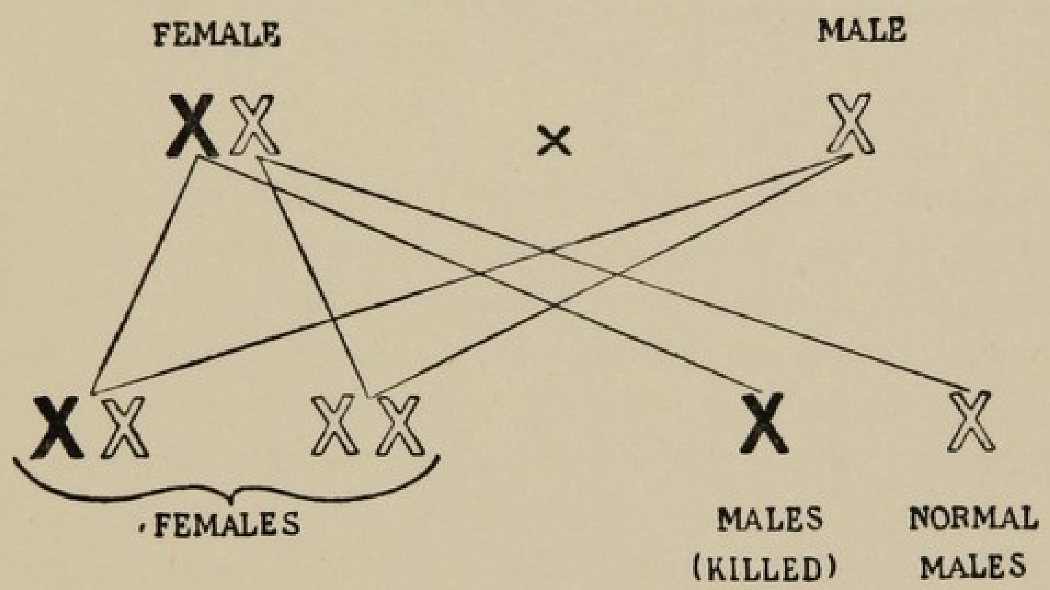


FIG. 24.—Inheritance of a sex linked lethal factor in Drosophila.

of the chromosomes, which so act as to prevent the normal physiological actions and reactions necessary for development and life.

The simplest case is that of a sex-linked lethal factor. The offspring from the mating of certain females of Drosophila give a sex ratio of two females to one male.

The explanation of this abnormality is that the lethal factor is a recessive, and therefore can only cause the death of the insect when alone. If present with its alternative non-lethal factor it is inoperative.

In Fig. 24 is shown the result of mating a female, one of whose sex chromosomes contains the lethal (shown in black) with a normal male. All the daughters survive because they receive a normal sex chromosome from their father, which prevents the lethal one doing harm. Half the sons on the other hand die because they have received the lethal-carrying chromosome.

There are now about twenty different lethal factors known in Drosophila; they act in various ways, some causing death in the egg stage, others death of the larvæ or pupæ.

IX

VARIATIONS: GERMINAL AND ACQUIRED

Types of variation—Inheritance of acquired characters—Early theories of variation—Continuous and discontinuous variation—Causes of variation—"Pure lines."

IT is now possible to review the facts presented in some detail in the foregoing chapters from the more theoretical point of view, namely as to their bearing on the broad issues of a theory of evolution.

As we have seen, all animals and plants spring from small particles, which are, in the plants, the spores or the seeds, and in animals the fertilized eggs. It is evident, therefore, that these small bodies must contain all the hereditary characters, for they are the sole agents for carrying on the species from generation to generation.

During development the egg or seed divides into other small bodies, the cells, which will form the adult body. In other words, the cells become differentiated, giving rise to the various organs, tissues, etc., of the animal or plant. Thus in the end the vast majority of the cells have become so specialized that they can do only one thing: muscle cells contract, nerve cells conduct stimuli, bone cells form hard supporting structures, and so on. A few, however, namely the germ cells, undergo little modification: they remain practically the same as they were when first formed ; from them the next generation will be produced.

This leads to the interesting deduction that these cells are immortal : the body cells—muscle, bone, nerve, etc.—will eventually die ; but the germ cells will continue so long as the species remains, for each new animal or plant is the direct descendant of the germ cells of its parents.

These considerations led Weismann to the conception of germinal continuity, and the isolation of the germ cells from agents affecting the body cells. As Wilson expresses it :—" It is a reversal of the true point of view to regard inheritance as taking place from the body of the parent to that of the child. The child inherits from the parent germ cell, not from the parent body, and the germ cell owes its characteristics not to the body which bears it, but to its descent from a pre-existing germ cell of the same kind. Thus the body is, as it were, an offshoot from the germ-cell. As far as inheritance is concerned the body is merely the carrier of the germ cells which are held in trust for coming generations."

This idea is of great importance for a true understanding of the two great classes of variation to the consideration of which we must now return. The foregoing outline of Mendel's Law should help to give a mental picture of how germinal variations occur, although, admittedly, our knowledge of these facts is still only elementary. The whole question is of special interest as it leads to the controversy (now close on a century old) of the inheritance of acquired characters.

Germinal Variations.—These occur at the very beginning of the life of the organism, and though the variation may not appear until later, as, for example, one affecting the structure of the adult, yet the capacity for their production has been in the egg from the commencement. In other words they are variations of the germ plasm, that mysterious substance which passes from one generation to the next and is contained in the germ-cells.

These types of variation are in marked contrast to the second group known as somatic variations, which are impressed upon the body cells of the organism during its life by the action of the environment, and in many cases render the organism better fitted to its surroundings.

Acquired Characters.—It is well known that the continued use of an organ tends to increase its size and power. The muscles of a limb used for strenuous work enlarge ; and the skin, when continually exposed to sunlight, assumes a deeper colour than when it is covered.

The question now arises : has this kind of variation in the individual any effect on the race ; can it be handed on to the offspring ? Will the foal of the trotting horse inherit the muscular enlargement acquired by the parent ?

Quite apart from the absence of any definite physiological process so far discovered by which body changes could be transmitted to the nuclei of the germ-cells, other evidence in support of the inheritance of acquired characters is unsatisfactory in that it is almost always capable of interpretation in more than one sense, or else is of an indirect nature.

Take the well known flat fish such as flounders and soles, which both swim and lie on the sea-bottom. The uppermost side of the body is coloured and the under one colourless. This loss of pigment was supposed to be due to the cutting off of the light.

In a well-known experiment Cunningham reared flat fish in a tank lighted from below. The young fish, which are uniformly coloured, settled on the bottom, and at first the colour disappeared, but when the experiment was continued long enough the colour returned. The disappearance at the beginning proved that the loss was inherited, and Cunningham interprets the return as due to a reversal of the process. He concludes that the loss of pigment was originally due to the absence of light, and has gradually become hereditary. This is, however, only an assumption for which there is no proof.

A second type of indirect evidence is that of instincts, which are similar to deep-rooted habits. It has been suggested that here proof is afforded of the inheritance of acquired characters. Again, however, the evidence is unsatisfactory, as the worker-bee demonstrates. This insect has exceedingly well-developed instincts, but never reproduces itself. It is always produced by a queen and a drone (male bee), which possess instincts quite dissimilar from those of the worker.

If then we have a case like the above, where instincts are perfectly well developed, but where the inheritance of acquired characters is entirely ruled out, it seems unlikely that instincts in other species have arisen in this way.

Moreover it has still to be proved that instincts have arisen as acquired characters.

The direct evidence also is not satisfactory, doubtless in part owing to the difficulty in devising crucial experiments, and, as regards the higher animals, the length of time necessary for obtaining many generations.

Recently the whole question has been revived by some remarkable experiments made by Kammerer on salamanders and a species of frog, and by Guyer in America on the effect on the eyes of young rabbits of the introduction of certain substances into the blood stream of the mother. The interpretation of the results of these experiments has, however, been criticized in a very interesting way by other observers.

Prof. Goodrich pointed out in the case of Kammerer's frogs and proteus, that the character in question was not new to the race, but was one which had been lost. In Prof. Cunningham's flat fish the same type of character is being dealt with—the ancestors of the flounder were coloured alike on both sides, and, indeed, the young of the fish still have pigment above and below. The facts observed, therefore, may be interpreted as follows: the skin cells of the underside of the flounder originally had a factor reacting to the stimulus of light by producing pigment; this character made no difference to the life of the species living habitually on the sea bottom, and was, therefore, so to speak, withdrawn from the action of natural selection. It has been retained in a considerable degree through untold generations in the germ-plasm, and by the fresh application of the stimulus of light is called out once more. This argument is applicable to all cases so far adduced.

Guyer's experiments are the more interesting, for here there does seem to be an indication that the substances introduced into the blood stream have affected the germ plasm.

The present position then respecting this much-disputed question is that the cases so far brought forward are not sufficiently definite to warrant the acceptance of the belief that acquired characters are inherited.

The assumption is frequently made, especially in human affairs, that the environment is an important factor in shaping the individual. To a certain extent this is true, for the environment undoubtedly plays the main part in determining whether the capabilities of a man or woman are allowed to develop, but the environment alone will never create such capabilities.

Education will not produce a brilliant mathematician, historian or writer unless the potentialities for such work are already resident in the germ cells, but it is equally true that without education such potentialities will never reach fruition. Modern research is doing more and more to show that to be "well born" is half the battle of life.

Since germinal variations are inherited variations they are of importance for natural selection. They have been divided into two classes.

(*a*) Continuous
(*b*) Discontinuous

Continuous Variations.—If a character is chosen, which can be accurately measured, as, for example, human stature, and if a large number of individuals are observed, it will be found that there is a range of variation, and that this range is a graded one; it is continuous, showing no breaks between the tallest and the shortest individuals. Further, in continuous variation it will be found that one particular size is more common than another, and that as the sizes recede more and more from this most frequent value so the number of individuals of any particular size are fewer and fewer. For example, if sufficient cases are taken it is found that the height of men of a given race ranges with continuous gradations, from 57 to 77 inches. The measurement of 8,585 men, grouped in two-inch intervals, is given in the table. The greatest number of men fall between the limit 67–69 inches, and as the height differs from this value so there are fewer men having it.

Inches.	*No. of Men.*
57–59	6
59–61	55
61–63	252
63–65	1,063
65–67	2,213
67–69	2,559
69–71	1,709
71–73	594
73–75	111
75–77	21
77	2
	8,585

This grouping into two-inch limits is purely arbitrary; if the grouping had been made to the nearest inch or half-inch the general result would have been the same.

A convenient way of representing this type of variation is to construct a curve on squared paper, marking successive heights from 57–77 inches along a base line and the numbers of individuals having each height along the vertical (ordinate) line. By joining the points a curve is obtained like that of Fig. 25. The highest point represents the mode, or most frequent height, and the extreme variations from it tail out on each side towards the base line. A curve of this kind, which is similar on each side of the longest perpendicular (median), is known as a "normal curve," and is obtained whenever measurements, varying fortuitously around the most frequent value, are plotted. Variations

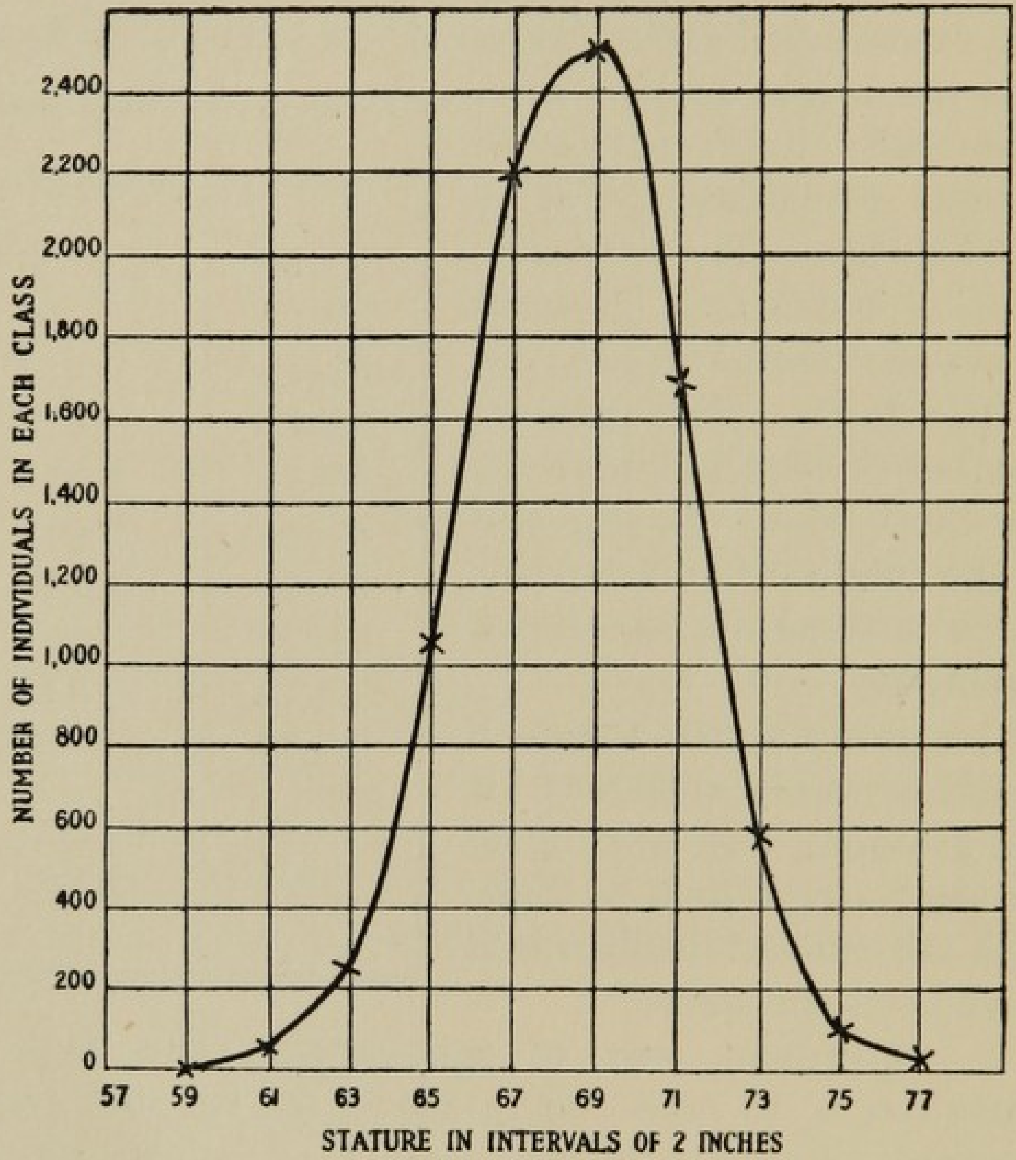


FIG. 25.—Frequency distribution of stature, showing the number of men of each height, the greatest number being 67–69 inches.

giving this type of curve are exceedingly common and are known as "normal" variations.

Many characters, however, have a slightly different type: different in that the frequency of variation below the mode is not equal to the frequency above it, in which case on one side of the modal value the curve will be steeper than on the other, and consequently the average value for the character (mean) will not be identical with the mode as is the case with the normal curve.

No. of Petals	*Frequency*
5	790
6	96
7	34
8	9
9	6
10	2
11	2
	939

Finally, there are extreme cases in which the mode is pushed to one end of the curve, and variations occur only on one side of it. A familiar example is the number of petals of the marsh marigold. The most frequent number is five (modal value), but there may be six, seven, or even eight; but never less than five. Graphically this variation will be a half-curve, as shown in the table and Fig. 26.

From the above examples it should be clear what is meant by continuous variations. This is the type which Darwin regarded as of extreme importance in evolution.

Discontinuous Variations.—These are not so common as the kind just considered, but it has been shown already that they are of great importance when inheritance is discussed, and they include some of the Mendelian characters studied. They are often termed sports, or saltations or mutations. As the term implies, these variations involve definite and usually considerable differences. In mankind it sometimes happens that children are born possessing six, seven or eight fingers, and extra toes are not unknown.

Also in cattle, horses, etc., animals with extra digits are at times born, or pigs having a solid digit instead

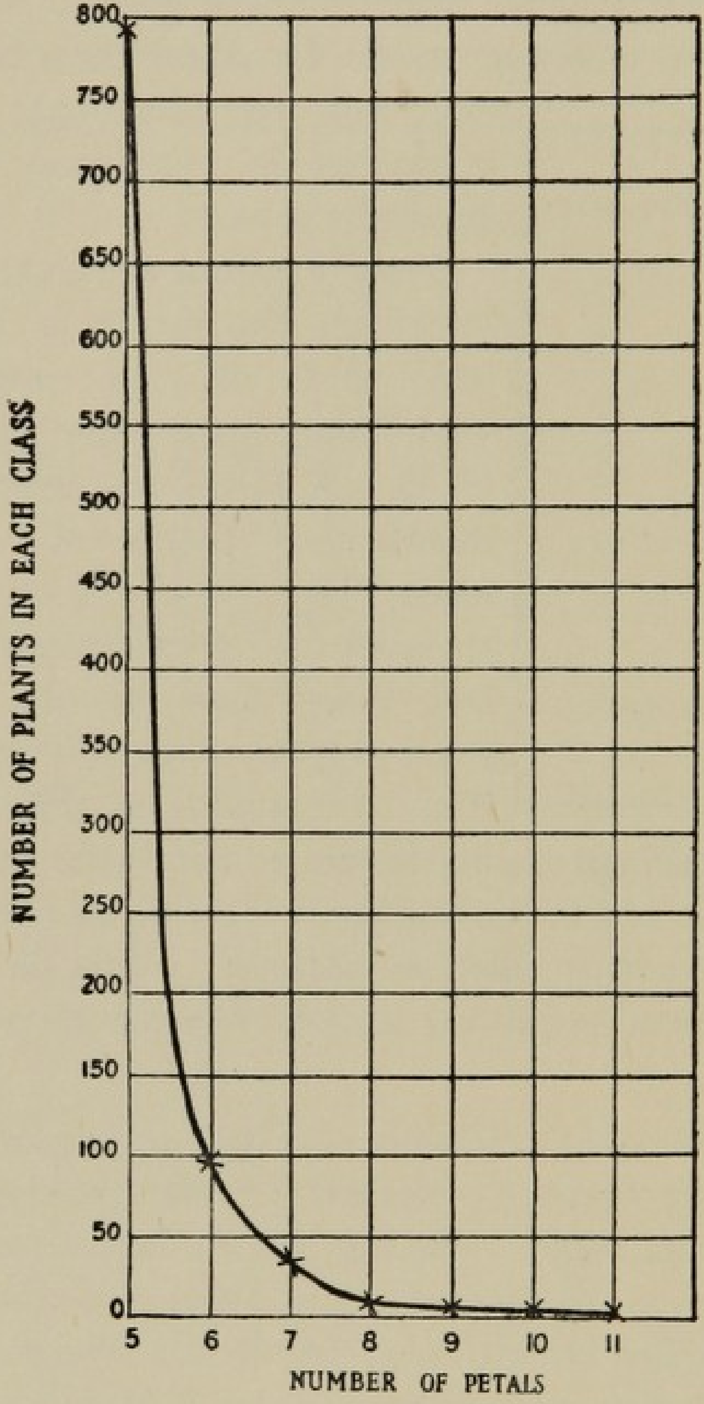


FIG. 26.—Frequency distribution of the number of petals of *Ranunculus bulbosus*: the greatest number being 5.

of two toes to each foot. A four-horned sheep is another example well known to farmers. Variations where parts are repeated are apt to occur in any structure composed of a numerical series of parts like the backbone, or the earthworm's body.

Other instances of discontinuous variation are not of this kind, for they are changes of the actual constitution of the parts concerned. They are substantive changes. For example, a plant usually having coloured flowers will produce offspring with white flowers, or the actual shape of the flowers may be modified. The famous breed of Ancona sheep is another example. A ram with markedly short legs suddenly appeared in America in 1791, and it was found that the peculiarity was inherited, with the result that a short legged race of sheep was developed incapable of jumping fences.

Causes of Germinal Variation.—Very little is accurately known about the causes of variation, except in the case of acquired characters, where it is obvious that they are brought about by the environment acting directly upon the body.

As regards inborn germinal variations three theories have been brought forward :

(*a*) An inherent tendency for the germ plasm to vary ;
(*b*) Influence of environment directly on the germ cells ;
(*c*) The action of crossing different races or species.

As regards the first, certain variations undoubtedly arise in this way, but this is no explanation as to how they occur.

Also nothing is definitely known of the nature of the possible effects of the environment on the germ cells. Certain experiments on insects give reason for supposing that moderate degrees of heat and cold may be capable of influencing the germ cells ; and recently it has been stated that slight treatment by radium or other external agents has an effect. It must be admitted, however, that such experiments are incomplete.

The effect of crossing in producing variation is so marked that some biologists have gone so far as to assert that it is the main cause ; but such a view is too sweeping, for there are asexual organisms having no union of the male and female elements in the production of young forms, but in which variations occur as definitely as in sexual species.

Pure Lines.—Mention must now be made of some remarkable experiments on beans made by a Danish biologist, Johannsen. Since the bean plant is one that can be self-fertilized, the complication introduced by the action of pollen from another flower was avoided.

All the descendants arising from self-fertilized single plants were called pure lines, and the individuals of each pure line showed for seed weight a normal variation about the mean value such as was the case with the height of men. Also the seed weight of the various pure lines taken together, that is the general population of the bean plants, gave a normal variation curve, the mean of which, however, was not identical with those for the pure lines. If the flowers of a plant belonging to any of the pure lines are self-fertilized, the mean seed weight of the offspring will be identical with that of the beans on the parent plant. In other words it makes no difference whether, within a pure line, a plant with heavy seeds or one with light seed is chosen as parent; the mean value for the seed weight of the offspring will not be increased or decreased; heaviness or lightness are not inherited. Selection within a pure line has no effect in altering the mean weight of the seeds.

Similar results have been obtained in animals by American zoologists.

If then selection within a pure line is without effect, how is it that breeders are successful in changing the types? The answer is that the animals and plants the breeder uses constitute a mixed population, and by selection the various pure lines are gradually separated; some are of poor quality and are therefore discarded, while the high quality ones are retained; but once such a line is isolated selection will be useless unless fresh blood is introduced from another line.

But more important is the fact that during the past few years it has been found that stable germinal variations take place within the pure lines. Thus a fresh starting point is offered for a new advance

X

BIOMETRY

Co-efficient of correlation—Law of ancestral heredity.

IN the study of heredity two methods of investigation are possible. On the one hand a particular character may be examined in a large number of individuals and their descendants, and deductions then drawn as to the extent to which inheritance has taken place. An alternative method is to study intensively the character in a few individuals, noting the manner and extent to which it is transmitted from parents to children. The first method is a statistical one and constitutes a branch of the study of heredity known as biometry. Since a considerable amount of mathematical knowledge is needed to use it, only one or two of the more important principles will be discussed here; with the second method the reader is now sufficiently familiar, as it is the one adopted in Mendelian experiments.

The founder of biometry was Sir Francis Galton (who also originated the study of Eugenics), and the leading exponent of it in Great Britain has for many years been Professor Karl Pearson.

Co-efficient of Correlation.—This statistical method is most useful for measuring the degree of inheritance of characters, and though the mathematics required for finding its value are beyond the scope of this book, its significance and meaning may be explained.

In the last chapter it was seen that a human height varies from 57–77 inches and the most frequent height (modal value) is 68 inches. If the sons of a large number of men having a certain height, say 59 inches, are collected and measured their heights will form a normal frequency curve like that of Fig. 25. Now if the average height of the sons equalled that of their fathers, that is, if they diverged as far from the modal value of the general population as their father did, then the inheritance of short stature 59 inches would be complete. But if the modal value for the sons equalled that of the general population of men, that is 68 inches, there would have been no inheritance of short stature. The same reasoning, of course, holds for any height that might be selected for discussion.

In practice it is found that neither of the above possibilities occurs ; for the modal value for the sons of fathers of a given height is intermediate between that of the general population and the paternal height. That is, the average height of children of very tall or very short fathers tends towards the normal average height. This is called "regression." This does not mean that all children of short fathers will be taller than their fathers ; some will be taller, some shorter and some as short, but the average height of such children will be greater.

A little consideration will make evident that the amount of regression is an index of the degree of inheritance. A ratio, therefore, between the deviation from the mean of the sons and that of their fathers will be a measure of the inheritance of the characters considered.

Such a ratio is termed the "co-officient of correlation."

A complete resemblance between the fathers and sons would have unity as the co-efficient of correlation.

Pearson has calculated the co-efficients for stature for seven pairs of relations and finds that:

Father and son	=	0·514
Father and daughter	=	0·510
Mother and son	=	0·494
Mother and daughter	=	0·507
Brother and brother	=	0·511
Sister and sister	=	0·537
Brother and sister	=	0·553

The first four values are, however, a little too high, for it has been found that there is a marked correlation between husband and wives (0·28), in other words, that there is a tendency for people of a similar height to marry.

By using such mathematical methods Galton showed that mental qualities are inherited. Such work has since been greatly extended by Pearson and his collaborators.

Investigating such physical characters as health, eye colour, hair colour, head length, athletic power, of children born of the same parents, Pearson found the co-efficient of correlation to be 0·51. The mental characters — vivacity, assertiveness, introspection, popularity, conscientiousness, temper, ability—of the same children gave a correlation value of 0·52. It may be concluded, therefore, that mental characters as well as physical are matters of heredity.

It is commonly assumed that the environment plays an important part in determining the future characteristics of children ; to a certain extent this is true, but that heredity is the chief factor is becoming increasingly evident, witness another investigation of Pearson.

He tested the intelligence of children in Californian orphanages, where the environmental conditions were uniform, and that of children in schools in Great Britain under the varying conditions of school and home life. In the first case the co-efficient of correlation was 0·515 and in the second 0·508.

This result and many others pointing to similar conclusions are of great importance, for, as the late Prof. Doncaster wrote in "Heredity," "they show how little room is left in the development of the individual for the effects of environment even on the intellect or mind in the broadest sense of the word ; no doubt the direction which intellectual development takes is to a considerable extent determined by circumstances, but the kind of mind is irrevocably decided before the child is born. Still less is there room for the inheritance of the mental acquirements made by the individual during his life, and hence the hopes held out of improving the race by education and by special care of the dull or feeble-minded are illusory, except in so far as they improve the tradition. Just as the welfare of the race may be increased by an invention which is handed on from generation to generation, so the good effects of education or other improved conditions may be handed on, but this is not heredity. The father may educate his children because he himself was educated, but the mental powers of his children will be the same whether he had a good education or none. And the effects of special care given to the weakly or feeble-minded may be absolutely harmful to the race, if the improvement so effected leads to more frequent marriage among such unfortunates than would otherwise be the case, for then an increased number of defective children may be born, and the race-average be lowered. Hence has arisen the study known as 'Eugenics,' the study, that is, of the methods by which the race may be improved both physically and mentally. The whole trend of the results obtained is that in order to produce exceptionally gifted men in both body and mind, those with high development of the characters desired should be encouraged to marry; and that to prevent the production of the weakly and feeble-minded, the only method is to prevent such from having offspring. It is admitted that at present these things hardly come within 'practical politics,' but there is little doubt that the nation which first finds a way to make them practical will in a very short time be the leader of the world."

Law of Ancestral Inheritance.—When discussing the co-efficient of correlation consideration was given to the heights of sons of certain classes of fathers, without reference to the mothers. It is obvious, however, that since stature is an inherited character, the other parent will have an influence. The degree of inheritance due to both parents can, nevertheless, be estimated by comparing in any class the mean height of the two parents with the height of the sons and daughters. This mean height of father and mother is called the mid-parent.

When the co-efficient of correlation between the children and their mid-parent is calculated, it is found to be greater than when only one of the parents was considered, but still the inheritance is not complete, since the grand parents, great grand parents, etc. have not been taken into account. Galton investigated this point still further, and from a large amount of data, which he had collected, concluded that on the average the parents contributed $\frac{1}{2}$ of the heritage of an individual, the grand-parents $\frac{1}{4}$, the great-grand-parents $\frac{1}{8}$, the great-great-grand-parents $\frac{1}{16}$, and so on to the end of the series.

This Law of Ancestral Heredity has been re-investigated by Pearson, who concludes that in general it is correct, but modifies it in that he ascribes a greater parental contribution and a less ancestral one than Galton did.

In specific instances this law apparently does not hold ; but it must be remembered that it is a statistical one, not necessarily true for individual cases, but only when applied to large numbers, such as populations.

Much more is learned from the observation of individual single characters, as carried out in Mendelian experiments, than by statistical methods, but such observations are not always practicable.

This is strikingly the case where the character has a continuous variation, one modification overlapping the next ; and when experiment is impossible, as is the case with inheritance in Man.

The tendency has been, therefore, to use statistical treatment exclusively for continuous variations, though Pearson has applied such methods to certain characters showing discontinuous variation, such as the colour of horses, which are not capable of measurement. He finds that the inheritance of these characters can also be expressed in terms similar to those used for measurable ones ; but the method gives no clue to the physiological processes underlying the inheritance from generation to generation.

XI

VARIATION IN THE LIGHT OF MODERN RESEARCH

IN the preceding chapters a variety of topics has been considered, all of them having a distinct bearing on the question of evolution. It has been shown that the occurrence of evolution is beyond dispute, that the two fundamental properties of living matter on which it depends are variation and heredity; and an outline has therefore been given of the results of modern research on these two great principles. In conclusion it is fitting to see how this knowledge helps us to understand the way in which the various species of animals and plants have arisen.

Considering first of all variation, it is evident that new forms may arise simply by the recombination of Mendelian factors, similar to that which has been shown to occur when a cross is made between heterozygous tall purple-flowered sweet peas, the resulting offspring containing two new types, short purple and tall white. Also it is obvious that, as there are numerous factors concerned in the production of any living thing, the possible number of re-combinations, and therefore variations, is almost incalculable. The production of variations of this type may be compared to dealing a pack of cards. The number of cards is constant, but by repeated reshuffling the " hands " dealt are of different kinds.

Germinal Changes.—But variations of another sort can arise, namely, those due to actual modifications of the germ-cells ; there may, as we have seen, be changes in the number of chromosomes, or else in small parts of individual chromosomes, by some quite accidental rearrangement in division. Here new factors are added to the constitution of the organism, thus giving new possibilities for subsequent recombination. To continue the analogy, fresh cards are added to the pack, resulting in entirely different kinds of " hands " being dealt.

Such variations are the mutations referred to in an earlier chapter. Take, for example, the eye colour of Drosophila. The normal colour is red, but flies have appeared with differently coloured eyes ; and experiment has shown that these mutations are due to changes in a particular part of the X chromosome. Up to the present six different colours have arisen, representing modifications of the single unit factor red, and all are inherited in the usual Mendelian manner. The colours give the graded series : (1) red ; (2) blood ; (3) cherry ; (4) eosin ; (5) buff ; (6) tinged ; (7) white.

Thus a single unit factor may exist in numerous minutely differing grades, and the grades may give an almost continuous series. This is important, for it is often assumed that mutations must be of an extensive nature, occurring suddenly without intermediate stages ; that there is necessarily a sudden jump—a saltation. Such a view has been one of the arguments urged against accepting mutations as of importance in evolution, for the evidence shows that new species arise by gradual steps. That mutations are not necessarily large, however, is shown by the eye colour series of Drosophila, and by numerous other experiments. As Prof. Morgan has stated, " To-day we agree with Darwin that such extreme variations as those he called sports would rarely, if ever, have contributed to the formation of new types in nature. But we also know that minute differences also arise as mutants, and that these are inherited in the same way as are the larger mutant changes. It is also now clear that these smaller mutant variations must be those small heritable variations that Darwin himself appealed to as furnishing the materials of organic evolution."

Multiple Factors.—The discovery of "multiple factors" has also shown that the so-called continuous variations of the early observers arise by the action of separate Mendelian factors. The term is applied to those cases where several factors, which when acting alone give similar results, co-operate to increase the effect. Referring back to the series of eye colours in Drosophila, it has been found that one of them, eosin, can be modified by at least seven factors situated in different chromosomes. One of them lightens the colour and is called " whiting " ; another acts less intensely, giving cream " a," while a third produces a second shade of cream called " b." Three other factors, diluting the eosin, have been found ; and finally there is a darkening factor. The grades of eye colour, therefore, are considerable. There is a series ranging from red to white ; added to which seven factors are known giving gradation in one of the primary eye colours.

Primary Colours.	*Modifiers of Eosin.*
1. Red	1. Whiting
2. Blood	2. Cream a
3. Cherry	3. Cream b
4. Eosin	4. Diluter
5. Buff	5. Diluter
6. Tinged	6. Diluter
7. White	7. Dark

As yet in only one of the primary colours have the secondary factors been isolated, but it is not too bold to predict that as the years pass more and more gradations will be discovered, until all discernible shades have been distinguished, and it is not unlikely that each will be found to be dependent on a single Mendelian unit.

The height and length of the ear of Indian corn has also been shown to depend on multiple factors. Crosses between a long and short-eared strain gave intermediate plants; but in the F_2 generation the original types reappeared, connected by all intermediate lengths. This is shown in Fig. 27, where the ear lengths are represented as columns.

Again, the race of pigeons known as fantails are characterized by a large number of tail feathers, varying from 28 to 38; while other races have only 12. Crosses between the two give 12–20 tail feathered birds, which when crossed back to the fantail give offspring with 19–31 tail feathers. On the hypothesis that the fantail condition is due to the cumulative action of several factors, such results are easily understood.

Direct experimental evidence for multiple factors is not at present very great, but it is accumulating rapidly, and there is no doubt but that the future will

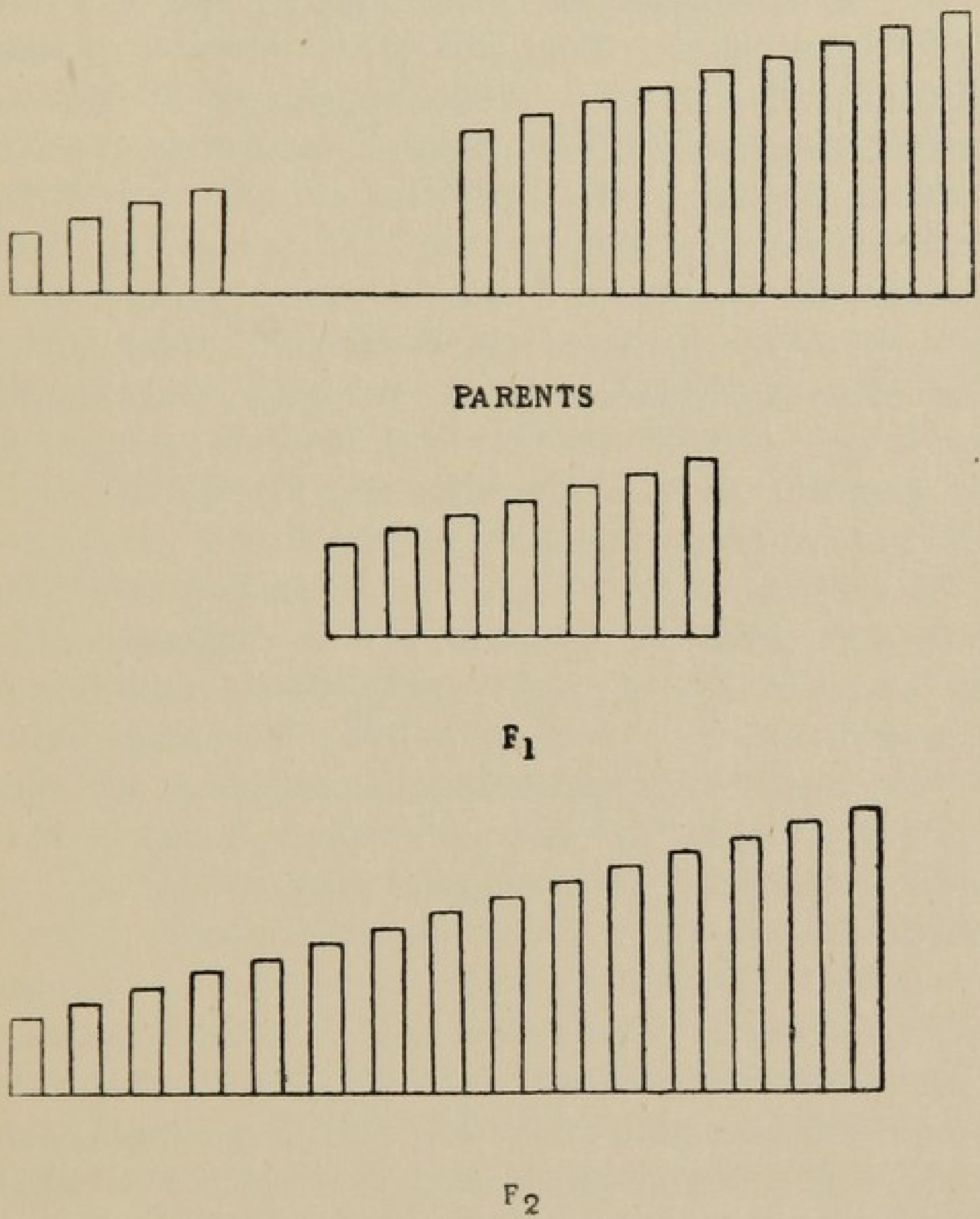


Fig. 27.—Action of multiple factors in producing continuous variations. Each column represents the average length of the ears of individual corn plants. Top line: at the left a short variety; at the right a long variety. Middle row: the F_1 generation from the cross of the above varieties. Lower row: the F_2 generation of the same cross

show that so-called continuous variations are mainly of this nature

It is easy to understand the occurrence of multiple factors when it is remembered how many factors must be involved in the building up of every single character. For instance, human stature, already adduced as a good example of a character studied biometrically, depends on numerous qualities, such as the size of the cells of the leg bones, vertebræ etc., on the curvature of the spine, on the amount of deposition of bone or cartilage, and so on. It is not to be wondered at, therefore, that a complete Mendelian analysis has not as yet been made for this character ; though the fact that it gives evidence for the Law of Ancestral Heredity is a further indication that very many factors are concerned.

To sum up, conception of multiple factors teaches that any character depends for its appearance on the co-operation of many independent factors. In Drosophila red eye colour results from the action of at least twenty-five factors ; if one of these changes (mutates) a different colour results. It is this one different factor that is regarded as a unit ; though at the same time the other twenty-four are necessary. There is, however, the converse case that a single factor may act on more than one character.

Failure to realize this has given rise to the statement that Mendelism and evolution are disconnected, since many of the characters showing Mendelian inheritance are of only slight importance to the animal or plant. Such a view is not warranted, for though a character, such as the number of bristles on the thorax of a fly, may be of little value, yet it is probable that the factor for that character also influences some vitally important function associated with the length of life. The factor for reduced wings in Drosophila affects also the legs, the length of life, and the number of eggs laid.

Further, a change in a factor, however slight, reacts on the whole of the body. A great variety of characters may be affected, some to a slight extent, others very conspicuously. These last are noticed and the factor named from them; though possibly the characters which are only slightly changed are those most important to the well-being of the organism.

For example, a mutation causing a change in a factor controlling the ductless glands of the body may produce changes of the utmost importance. These small structures throw into the blood certain secretions which have far-reaching effects. Thus, over development of the thyroid causes goitre, while a deficiency of the secretion gives rise to an abnormal mental condition called cretinism. Another small organ, the pituitary, situated in the brain, has a special influence on growth. Deficiency of the secretion causes the appearance of individuals, in whom during their period of development the growth of the skeleton is too rapid, so that they attain an abnormal stature. Such are the persons exhibited at shows and fairs as "giants." The condition is also associated with abnormalities of skin texture and hair development, together with deficiency in muscular power.

Other glands, related to equally important functions, also occur, such as the supra-renals; but the two examples given are sufficient to demonstrate how a change in the factor controlling any one of them will affect the whole of the body.

Effect of Selection.—Having seen that many inherited, i.e. germinal, variations are probably due to the interaction of multiple factors, it is necessary to consider what action selection can have in changing the type. In this connection there is one experiment of particular interest, for the results were at first quoted as a proof that selection can change a unit character. This conclusion has now been abandoned and the case recognized as one of multiple factors.

There are races of rats known as " hooded " in which the body colour is white, but the head and shoulders coloured, with a stripe running down the middle of the back. The extent of the hooded character is extremely variable ; in one direction the animal is almost entirely coloured except for a white stripe on the under surface ; and in the other direction the pigment is confined to the head.

The effect of selection on a mixed population of hooded rats was tested by experiment. In one case the selection was in a plus direction (towards the dark type), in the other case in the minus direction (towards the light type) ; and during the thirteen generations of the experiment steady progress was made towards the types required.

Another experiment, in which selection was made for the number of bristles on Drosophila, was equally effective in changing the types. Both these results were due to the sorting out of pure lines.

There is no doubt that selection can act within a mixed population, but, as already pointed out, there comes a time when the limit is reached, and further selection brings no further change. The pure lines of beans raised by Johannsen furnish an interesting example of the fact that this limit is reached more quickly in self-fertilized organisms. When the experiment started the bean population was a mixed one, containing many multiple factors ; selection, as in the case of the hooded rats, at the beginning was effective, but as the number of generations increased so the factors become more and more sorted out, until finally races were established pure (homozygous) for certain factors. When this stage was reached further selection was without effect. If this were the complete story it would seem that evolution by the selection of Mendelian factors could not have taken place, for though the number of possible new combinations of existing factors is enormously great, yet they are finite. The apparent difficulty is not serious, however, for it is certain that at rare intervals mutations, that is new factors, appear, rendering possible an entirely new set of combinations.

The fate of any particular new variation, therefore, is determined by whether it gives any general advantage or disadvantage to the organism in its struggle for existence. Of course, markedly disadvantageous factors, such as dominant lethals,[1] will rapidly disappear in a state of nature, but a moderately disadvantageous one will be gradually eliminated, the creatures possessing it becoming rarer and rarer, finally reaching a state of almost complete extinction.

The variation, on the other hand, which confers an advantage in the struggle for existence, will become more and more widely spread through the population ; the rate of increase becoming more rapid as the number of individuals possessing it increases. Finally in certain cases the new type will replace the original one.

[1] See p. 106.

Of the variations, therefore, which are of importance in evolution by Natural Selection there are at least two kinds—the commonest due to the recombination of already existing factors, the rarest due to the introduction of new factors by changes in the constitution of the chromosomes. These two are intimately connected.

Since Mendelian factors do not blend, but segregate completely one from the other, the amount of variability within a species would increase without limit if mutations were continually occurring. Furthermore, the appearance of mutants is sufficiently rare to counteract the diminution of variability which continual selection in the same direction produces.

This leads to the final point, viz. the importance of sexual reproduction for maintaining the variability of a species by the continual segregation and redistribution of the Mendelian factors. A mutant is of necessity an experiment; there is no directive action ensuring that it shall be for the good of the species: it may equally well be disadvantageous, as, for example, lethals. But in a population containing many different Mendelian factors, reproduction, which involves the union of two germ-cells, affords an excellent method for testing the many new combinations which a single mutation provides. Some of them may be of value, and will, therefore, by selection become predominant, and conversely, unfavourable combinations will be suppressed.

For such reasons it is difficult to believe that animals or plants producing sexually can adapt themselves readily to changing environmental conditions.

Those who have followed the argument through these pages will have realized that great advances have been made in the study of variation and heredity in their relation to evolution ; but there are still great gaps in our knowledge which can only be filled by the application of experimental methods to the solution of the problem. The whole cell system of an animal or plant is involved in the production of any character, but as regards the way in which these characters are inter-related, and how the developmental processes are arranged so as to ensure their appearance at the right time and in the correct position of the body, is still a mystery. As Wilson phrases it, " We are ready with the time-honoured replies : It is an act of the 'organism as a whole' ; it is a 'property of the system as such' ; it is 'organization.' These words, like those of Goldsmith's country parson, are 'Of learned length and thundering sound.' In the plain speech of every-day life their meaning is : We do not know."

In spite of this, however, the knowledge we do possess all points clearly in one direction ; the theoretical point which at first seemed hopeless of solution, namely, the origin of variations, is year by year becoming better understood. In fact, the theory of Evolution, propounded with such care by Darwin, is to-day that which is still receiving the greatest amount of experimental support.

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