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IN RELATION TO EVOLUTION AND ANIMAL BREEDING

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BY

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PREFACE

This little book is based on a course of eight lectures delivered in November and December, 1910, before the Lowell Institute, Boston, as well as on a course of five lectures delivered before the Graduate School of Agriculture held under the auspices of the Association of Agricultural Colleges and Experiment Stations at Ames, Iowa, in July, 1910. The hope is entertained that it may be of service to students and that it will also interest the general reader.

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W. E. CASTLE

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INTRODUCTION

GENETICS, A NEW SCIENCE

THE theory of organic evolution has probably influenced more fields of human activity and influenced them more profoundly than has any other philosophic deduction of ancient or modern times. By this theory philosophy, religion, and science have been revolutionized, while in the practical arts of education and agriculture, twin foundation stones of the state, man has been forced to adopt new methods of procedure or to justify the old ones in the light of a new principle.

The evolutionary idea has forced man to consider the probable future of his own race on earth and to take measures to control that future, a matter he had previously left largely to fate. With a realization of the fact that organisms change from age to age and that he himself is one of these changing organisms man has attained not only a new ground for humility of spirit but also a new ground for optimism and for belief in his own supreme importance, since the forces which control his destiny have been placed largely in his own hands.

The existence of civilized man rests ultimately on his ability to produce from the earth in sufficient abundance cultivated plants and domesticated animals. City populations are apt to forget this fundamental fact and to regard with indifference bordering at times on scorn agricultural districts and their workers. But let the steady stream of supplies coming from the land to any large city be interrupted for only a few days by war, floods, a railroad strike, or any similar occurrence, and this sentiment vanishes instantly. Man to live must have food, and food comes chiefly from the land.

A knowledge of how to produce useful animals and plants is therefore of prime importance. Civilization had its beginning in the attainment of such knowledge and is limited by it at the present day. If, therefore, this knowledge can be increased, civilization may be advanced in a very direct and practical way. Before Darwin the practices of animal and plant breeders were largely empirical, based on unreasoned past experience, just as was in antiquity the practice of metallurgy. Good plows and good swords were made long before a scientific knowledge of the metals was attained, but without that scientific knowledge the wonderful industrial development of this present age of steel would have been quite impossible. In a similar way, if not in like measure, we may reasonably hope for an advance in the productiveness of animal and plant breeding when the scientific principles which underlie these basic arts are better understood. Two practical problems present themselves to the breeder: (1) how to make best use of existing breeds, and (2) how to create new and improved breeds better adapted to the conditions of present-day agriculture. We shall concern ourselves with the second of these only.

The production of new and improved breeds of animals and plants is historically a matter about which we know scarcely more than about the production of new species in nature. Selection has been undoubtedly the efficient cause of change in both cases, but how and why applied and to what sort of material is as uncertain in one case as in the other. The few great men who have succeeded in producing by their individual efforts a new and more useful type of animal or plant have worked largely by empirical methods. They have produced a desired result but by methods which neither they nor any one else fully understood or could adequately explain. So there exists as yet no true science of breeding but only a highly developed art which was practiced as successfully by the ancient Egyptians, the Saracens, and the Romans as by us. The present, however, is an age of science; we are not satisfied with rule-of-thumb methods, we want to know the *why* as well as the *how* of our practical operations. Only such knowledge of the reasons for methods empirically successful can enable us to drop out of our practice all superfluous steps and roundabout methods and to proceed straight to the mark in the most direct way. The industrial history of the last century is full of instances in which a knowledge of causes in relation to processes, i. e. a *scientific* knowledge, has shortened and improved practice in quite unexpected ways. So we may not doubt the ultimate value in practice of a science of breeding, if such a science can be created.

A beginning has been made during the last ten years, starting with the rediscovery of Mendel's law of heredity in 1900. This book will be concerned largely with the operations of that law.

CHAPTER I

THE DUALITY OF INHERITANCE

AT the outset we may with profit inquire what is meant by heredity. When a child resembles a parent or grandparent in some striking particular, we say it *inherits* such-and-such a characteristic from the parent or grandparent in question. *By heredity, then, we mean organic resemblance based on descent.*

Resemblances due to heredity may exist even between individuals not related as ancestor and descendant, as for example between uncle and nephew. Here the resemblance rests on the fact that uncle and nephew are both descended from a common ancestor, and they resemble each other simply because they have both inherited the same characteristic from that ancestor. This form of inheritance is sometimes spoken of as collateral in distinction from direct inheritance. In all cases alike community of descent is the basis of resemblances which can be ascribed to heredity, whether direct or collateral. Mother and child, no less than uncle and nephew, resemble each other because they have received a common inheritance from a common ancestor.

Three biological facts of fundamental importance to a right understanding of heredity were known imperfectly or not at all in the time of Darwin and Mendel. These are (1) the fertilization of the egg, (2) the maturation of the egg, which must precede its fertilization, and (3) the non-inheritance of "acquired" characters. These we may consider in order.

Every new organism is derived from a preexisting organism, so far as our present experience goes. It may not have been so always. Indeed, on the evolution theory, we must suppose that living matter originally arose from lifeless, inorganic matter. But if it did, this may have occurred, and probably did occur, under physical conditions quite different from those now existing. At the present time the most exhaustive researches fail to reveal the occurrence of spontaneous generation, that is, the origin of living beings other than from pre-existing living beings.

In asexual methods of reproduction a new individual arises out of a detached portion of the parent individual. Such methods of origin are varied and interesting, but do not concern us at present. In all the higher animals and plants a new individual arises, by what we call a sexual process, from the union of two minute bodies called the reproductive cells. They are an egg-cell furnished by the mother and a sperm-cell furnished by the father.

There is a great difference in size between egg and sperm. The egg is many thousand times greater in bulk, as seen in Fig. 1, for example, yet the influence of each in heredity appears to be equal to that of the other. This fact shows unmistakably that the bulk of the reproductive cell is not significant in heredity. A large part of the relatively huge egg can have no part in heredity. It serves merely as food for the new organism, furnishing it with building material until such a time as it can begin to secure food for itself. The essential material, so far as heredity is concerned, is evidently found in egg and sperm alike. It is plainly small in amount and possibly consists merely in ferment-like bodies which ini-

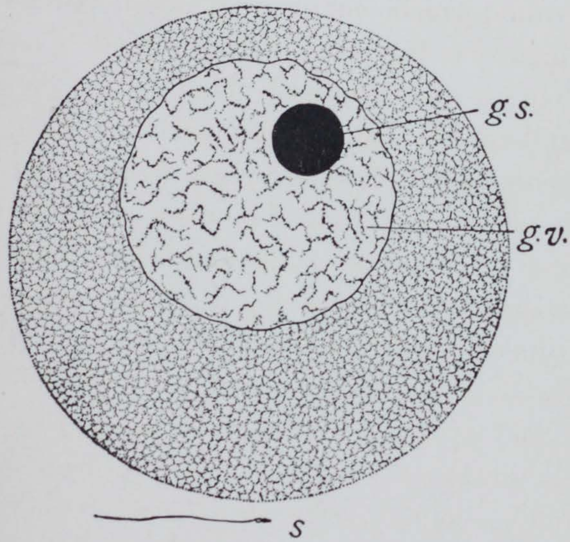


FIG. 1. — Egg and sperm (*s*) of the sea-urchin, *Toxopneustes*, both shown at the same enlargement. (After Wilson.)

tiate certain metabolic processes in a suitable medium represented by the bulk of the egg. The *amount* of a ferment used in starting a chemical change bears no relation, as is well known, to the amount of the chemical change which it can bring about in a suitable medium.

The equal share of egg and sperm in determining the character of offspring is well shown in the following experiment. An albino guinea-pig is one which lacks in large measure the ability to form black pigment. Apparently it does not possess some ingredient or agency necessary for the production of pigment. Now, if an albino male guinea-pig, such as is shown in Fig. 15, be mated with a black female guinea-pig of pure race, such as is shown in Fig. 14, young are produced all of which are black, like the mother, none being albinos, like the father. Fig. 16 shows black offspring produced in this way. Exactly the same result is obtained from the reverse cross, that is, from mating an albino mother with a black sire. It makes no difference, then, whether the black parent be mother or father, its blackness regularly dominates over the whiteness of the albino parent, so that only black offspring result. This fact, which has been repeatedly confirmed, shows that the black character is transmitted as readily through the agency of the minute sperm-cell as through the enormously greater egg-cell.

Let us now consider what happens when egg and sperm unite, in what we call the fertilization of the egg. The egg is a rounded body incapable of motion, but the sperm is a minute thread-like body which moves like a tadpole by vibrations of its tail. In the case of most animals which live in the water, egg and sperm-cells are discharged into the water and there unite and develop into a new individual, but in the case of most land animals this union takes place within the body of the mother. We may consider an illustration of either sort.

The fertilization of the egg of a marine worm, Nereis, is shown in Fig. 2. The thread-like sperm penetrates into the egg. Its enlarged head-end forms there a small nuclear body, which increases in size until it equals that of the egg-nucleus, with which it then fuses. The egg next begins to divide up to form the different parts of a new worm-embryo. To each of these parts the nuclear material of egg and sperm is distributed equally. Since this development takes place wholly outside the body of either parent it is necessary that the egg contain enough food to last until the young worm can feed itself. This food material is

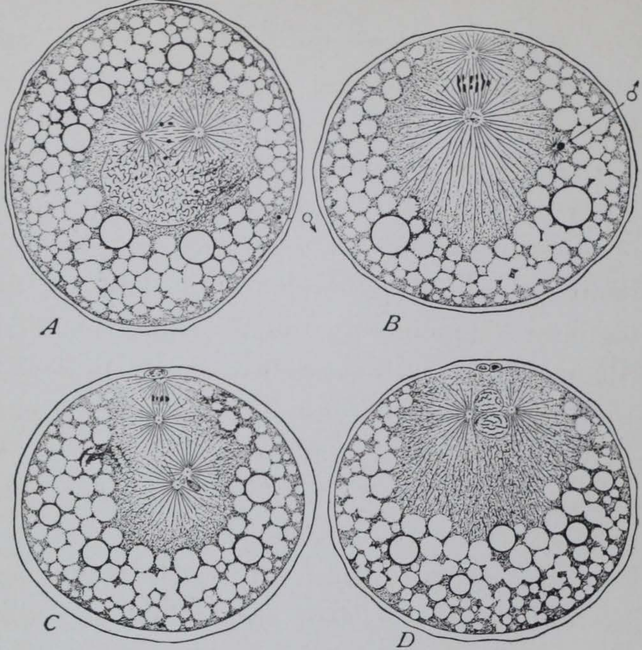


FIG. 2. — Fertilization of the egg of *Nereis*.

A. The sperm has entered the egg and is forming a minute nucleus at ♀. The egg-nucleus is breaking up preparatory to the first maturation division. *B*. The egg-nucleus is undergoing the first maturation division. Notice the conspicuous rod-like chromosomes separating into two groups. The sperm-nucleus (♂) is now larger and lies deeper in the egg. *C*. A small polar-cell has been formed above by the first maturation division of the egg. A second division is in progress at the same point. The sperm-nucleus is now deep in the egg and is preceded by a double radiation (amphiaster). *D*. Two polar-cells are fully formed. The matured egg-nucleus is now fusing with the sperm-nucleus. An amphiaster indicates that division of the egg will soon take place. (After Wilson.)

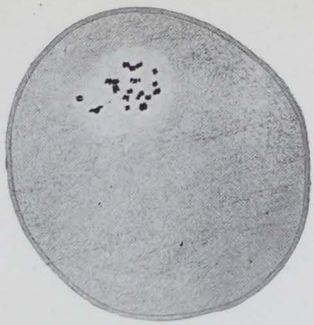
represented in part by the conspicuous oil-drops seen in the egg (the heavy circles in Fig. 2).

The egg of a mouse needs no such store of nourishment, since in common with the young of other mammals the mouse-embryo nourishes itself by osmosis from the body fluids of the mother. The mouse-egg is accordingly smaller. Stages in its fertilization are shown in Fig. 4. In *A* the sperm has already entered the egg. Remnants of its thread-like tail may still be seen there. Nearby is seen a nuclear body derived from the sperm-head. Opposite is seen the nuclear body furnished by the egg itself. The two nuclear bodies fuse and their united substance is then distributed to all parts of the embryo-mouse, just as happens in the development of the worm, Nereis.

There are reasons for thinking that the nuclear material is especially important in relation to heredity and that the equal share of the two parents in contributing it to the embryo is not without significance, for inheritance, as we have seen, is from both parents in equal measure. In cases where the inheritance from each parent is different it can be shown that the offspring possess two inherited possibilities, though they may show but one. Thus in the case of a black guinea-pig, one of whose parents was white, the other black, it can be shown that the animal transmits both qualities (black and white) which it received from its respective parents, and transmits them in equal measure. For, if the cross-bred black animal be mated with a white one, half the offspring are black and half of them white. The cross-bred black animal inherited black from one parent, white from the other. It showed only the former, but on forming its reproductive cells it transmitted black to half of these, white to the other half. Hence the cross-bred black individual was a duality, containing two possibilities, black and white, but its reproductive cells were again single, containing either black or white, but not both.

Now it has been shown in recent years that the nuclear material in the reproductive cells behaves exactly as do black and white in the cross just described. This nuclear material becomes doubled in amount at fertilization,

FIG. 3. — Egg of a mouse previous to maturation. (After Kirkham.)



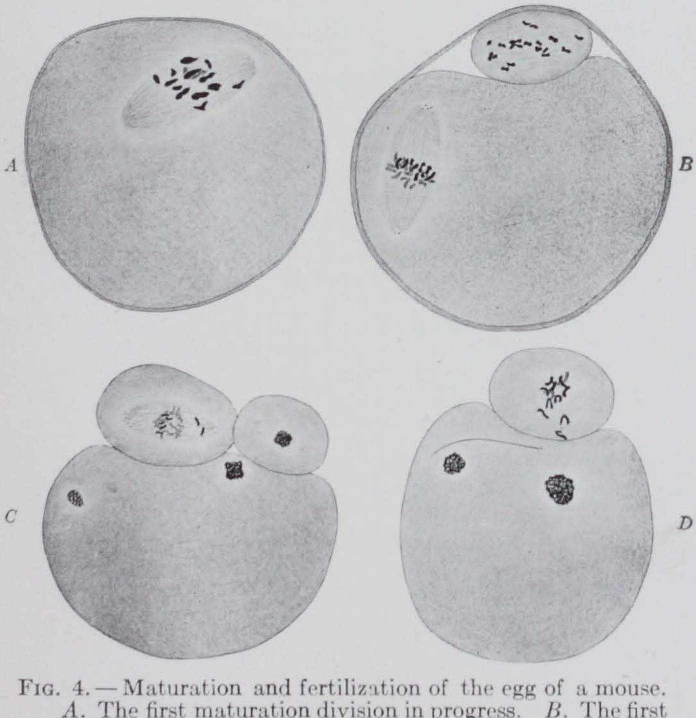


FIG. 4. — Maturation and fertilization of the egg of a mouse. *A*. The first maturation division in progress. *B*. The first polar-cell fully formed; the second maturation division in progress. *C*. The second maturation division completed; the second polar-cell is the smaller one; near it, in the egg, is the egg-nucleus, and at the left is the sperm-nucleus. *D*. A view similar to the last, but showing only one polar-cell, the second; note its twelve distinct chromosomes; near the sperm-nucleus in the egg, at the left, is seen the thread-like remains of the sperm-tail. (After Kirkham.)

equal contributions being made by egg and sperm. This double condition persists throughout the life of the new individual in all its parts and tissues. But if the individual forms eggs or sperm, these, before they can function in the production of a new individual, must undergo reduction to the single condition.

This reduction process is called maturation; it is well illustrated in the case of the mouse-egg, whose fertilization has already been described. The large nucleus of the egg-cell, as it leaves the ovary, is either broken up or about to break up preparatory to a cell-division. The most conspicuous of the nuclear constituents are some dense, heavily staining bodies called chromosomes, about twenty-four in number. In Fig. 3 each of these is split in two, preparatory to the first maturation division. The egg now divides twice, both times very unequally (Fig. 4), forming thus two smaller cells called polar cells, or polar bodies. They take no part in the formation of the embryo. The chromosomes left in the egg after these two divisions are only about half as numerous as before, or about twelve in number. These form the chromatin contribution of the egg to the production of a new individual. It is possible that other cell constituents undergo a similar reduction by half during maturation, but of this we have no present knowledge.

The known fact of chromosome reduction, of course, favors the current interpretation that the chromosomes are bearers of heredity, though it by no means proves the correctness of that interpretation. In the egg of Nereis, as well as in that of the mouse, two maturation divisions precede the fertilization of the egg. See Fig. 2. In *B* the first maturation division is in progress; in *C* the second is in progress; and in *D* both polar cells are fully formed, while egg and sperm nuclei are uniting. Similar processes occur in eggs generally, prior to their fertilization.

Like changes occur also in the development of the sperm-cells. In Fig. 5 the original or unreduced condition of the chromosomes in a cell of the male sexual gland is shown (at *A*) as one of four chromosomes to a cell. After a series of changes involving as in the maturation of the egg two cell-divisions, we find (at *H*) that the products of the original cell contain in each case two chromosomes, half the original number.

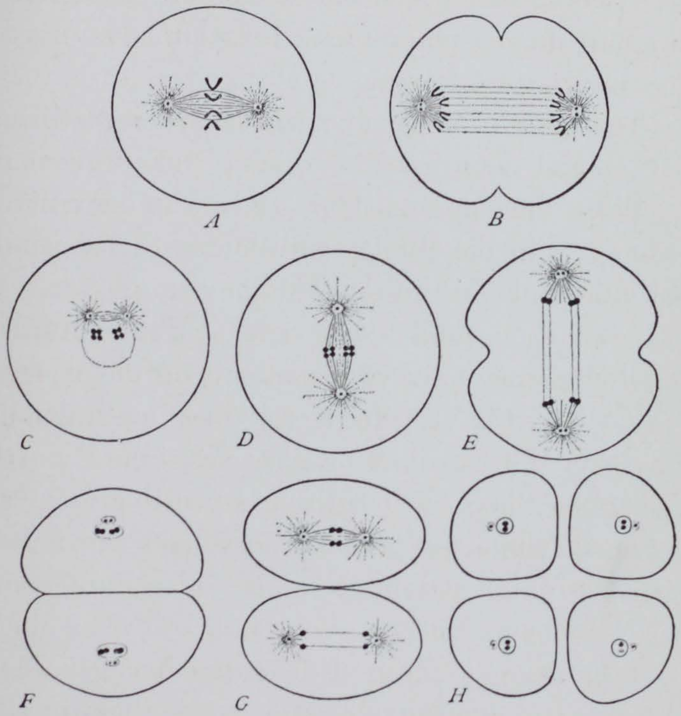


FIG. 5. — Diagrams showing the essential facts of chromosome reduction in the development of the sperm-cells. (After Wilson.)

These chromosomes make up the bulk of the head of the sperm which forms from each of these cells, its tail being derived from other portions of the cell.

It follows that not only eggs but also sperms, prior to their union in fertilization have passed into a reduced or single state as regards their chromatin constituents, whereas the fertilized egg, and the organism which develops from it, is in a double condition. It will be convenient to refer to the single condition as the N condition, the double as the 2 N condition.

From a wholly different source we have evidence strongly confirmatory of the conclusion that the fertilized egg contains a double dose of the essential nuclear material. By artificial means it has been found possible to cause the development of an unfertilized egg. The means employed may be of several different sorts, such as stimulation with acids, alkalies, or solutions of altered density. In such ways the development has been brought about of the eggs of sea-urchins, star-fishes, worms, and mollusks, which normally require fertilization to make them develop.

The sea-urchin egg has been made to develop more successfully than any other. This has occurred even after the egg had undergone maturation, being reduced to the N condition. From the development of such reduced but unfertilized eggs fully normal sea-urchins have been obtained which even contain developed sexual glands. On the other hand it has been found possible to break the egg into fragments by shaking it, or cutting it into bits with fine knives or scissors. It has also been found possible to bring about the development of an egg fragment so obtained, — a fragment which contained no egg nucleus. This result has been attained by allowing a sperm to enter it and form there a nuclear body. No adult organism has yet been reared from such a fertilized egg-fragment, but so far as the development has been followed it progressed normally.

There can accordingly be no doubt that the nuclear material of a sperm-cell has all the capabilities of that of an egg-cell and can indeed replace it in development. Accordingly, when, as in normal fertilization, both an egg nucleus and a sperm nucleus are present in the cell, a double dose of the necessary nuclear material is supplied. The second or extra dose is, however, not superfluous. It probably adds to the vigor of the organism produced, and in some cases at least, materially affects its form. For many animals and plants exist in two different conditions, in one of which the nuclear components are simple, N, while in the other they are double, 2 N. Thus in bees, rotifers, and small crustacea the egg may under certain conditions develop without being fertilized. If the egg develops before maturation is complete, that is in the 2 N condition, the animal produced is a female, like the mother which produced the egg. But if the egg undergoes reduction to the N condition before beginning its development, then it produces a male individual, an organism, so far as reproduction is concerned, of lower metabolic activity.

In many plants, too, individuals of N and of 2 N constitution occur, which differ markedly in appearance. Thus the ordinary fern-plant is a 2 N individual, but it never produces 2 N offspring. Fig. 6 shows an ordinary fern-plant, which produces spores on the under

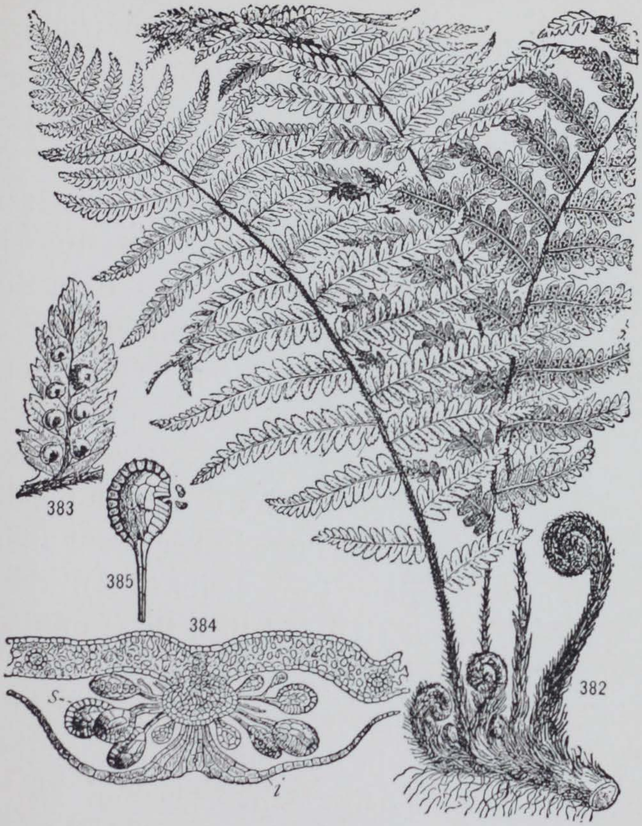


FIG. 6. — An ordinary fern, which reproduces by asexual spores. The fern is shown reduced in size at 382; a portion of a frond seen from below and slightly enlarged, at 383; a cross-section of the same more highly magnified, at 384. Notice in 384 the sporangia, and in 385 one of these discharging spores. (After Wossidlo, from Coulter Barnes and Cowle's Textbook of Botany.)

surface of its fronds. Each of those spores is a reproductive cell which, like the mature eggs and sperm of animals, is in a reduced nuclear condition (N). These spores germinate, however, without uniting in pairs and form a plant different from the parent, just as the mature egg of a bee, if unfertilized, develops into an individual different from the parent, in that case a male. The plant which develops from the spore of a fern is small and inconspicuous and is known as a prothallus. See Fig. 7. It produces sexual cells (eggs and sperm) which, uniting in pairs, form fern-plants, 2 N individuals. Thus there is a constant alternation of generations, fern-plants (2 N), which produce prothalli (N), and then these produce again fern-plants (2 N).

The fact is worthy of note that in an animal or plant which is in the single or N condition, there occurs no chromatin reduction at the formation of reproductive cells. Its cells are already in the single condition, and they probably cannot be further reduced without destroying the organism. The 2 N fern-plant forms reproductive cells, its spores, which are in the reduced condition, N, and these germinate into the prothallus, which accordingly is

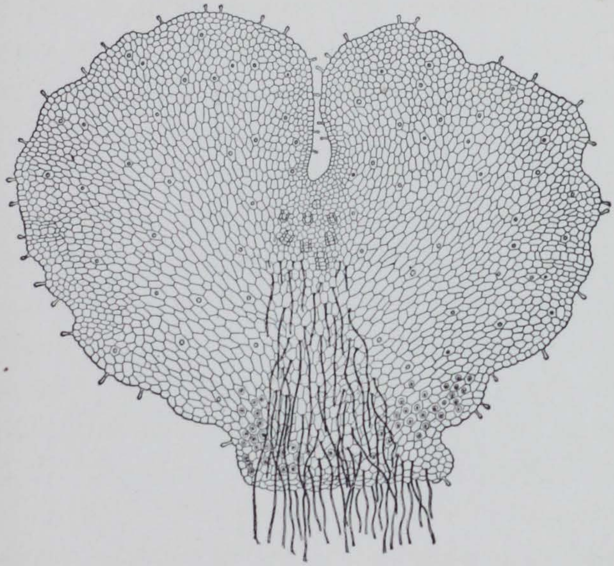


FIG. 7. — The prothallus of a fern, which reproduces by sexual cells, eggs and sperm. The eggs are borne in the sac-like "archegonia," just below the notch in the figure. They, like the sperm-forming "antheridia," lie on the under surface of the flattened prothallus which is here viewed from below. Notice the root-hairs or rhizoids by which the plant feeds. Highly magnified. (After Coulter, Barnes, and Cowles.)

N throughout. But when the prothallus forms reproductive cells, no reduction occurs. Its egg-cells and its sperm-cells in common with all other cells of the prothallus are already in the reduced condition without any maturation divisions. The result of their union in pairs, at fertilization, is the formation of 2 N combinations that germinate into fern-plants.

Similarly in the case of a male animal which

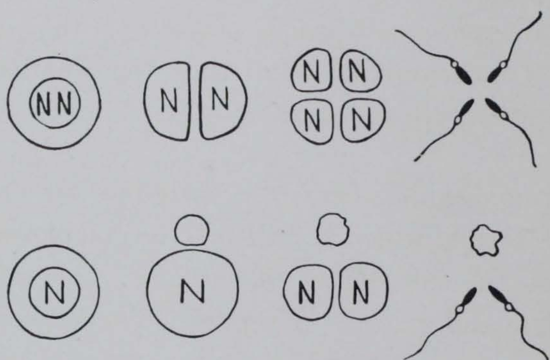


FIG. 8. — Diagram showing the chromosome number in the spermatogenesis of ordinary animals (upper line) and of the wasp (lower line).

has developed from a reduced but unfertilized egg, no reduction occurs at the formation of its sperm-cells. In an ordinary male animal, one which is in the double or 2 N state, the development of the sperms is attended by reduction to the N condition. In this process there occur two cell-divisions producing from each initial cell four sperms. See Fig. 5, and

Fig. 8, upper line. But in the male wasp, whose cells are in the N condition at the beginning, one of these divisions is so far suppressed that the resulting cell products are of very unequal size, and the smaller one contains no nuclear material. The other then gives rise to two sperm-cells, each possessing the original N nuclear condition, while the small non-nucleated cell degenerates. See Fig. 8, lower line.

In conclusion, I wish to introduce two technical terms, which it will be convenient for us to use in subsequent discussions. These are *gamete* and *zygote*. A reproductive cell (either egg or sperm) which is in the reduced condition (N) ready for union in fertilization is called a gamete. The result of fertilization is a zygote, a joining together of two cells each in the N condition. The result is a new organism, at first a single cell, in the 2 N condition.

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CHAPTER II

GERM-PLASM AND BODY, THEIR MUTUAL INDEPENDENCE

IN the last chapter we discussed two biological principles which, if clearly grasped, greatly simplify an understanding of the process of heredity. These are as follows:

(1) A sexually produced individual arises from the union of two reproductive cells (or gametes), each of which contains, so far as heredity is concerned, a full material equipment for the production of a new individual. Accordingly, the newly produced individual is two-fold or duplex as concerns the material basis of heredity.

(2) If the new individual becomes adult and forms gametes, the production of these will be attended by a reduction to the simplex or single condition as regards the material basis of heredity.

To these two principles we may now add a third, viz.: —(3) The individual consists of two distinct parts: first, its body destined to die and disintegrate after a certain length of time; and, secondly, the germ-cells contained within that body, capable of indefinite existence in a suitable medium.

The fertilized egg or zygote begins its independent existence by dividing into a number of cells. These become specialized to form the various parts and tissues of the body, muscle, bone, nerve, etc., and by becoming thus specialized they lose the power to produce anything but their own particular kind of specialized tissue; they cannot reproduce the whole. This function is retained only by certain undifferentiated cells found in the reproductive glands and known as germ-cells. They are direct lineal descendants of the fertilized egg itself. If they are destroyed the individual loses the power of reproduction altogether.

External influences which act upon the body may of course modify it profoundly, but such modifications are not transmitted through the gametes, because the gametes are not derived from body-cells, but from germ-cells. This relationship first pointed out by Weismann may be expressed in a diagram, as in Fig. 9. Only such environmental influences as directly alter the character of the germ-cells will in any way influence the character of subsequent generations of individuals derived from those

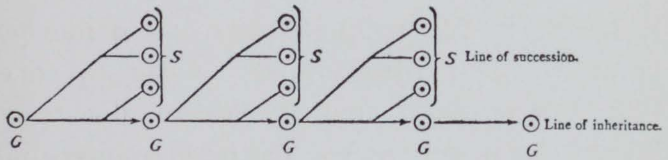

FIG. 9. — Diagram showing the relation of the body (S) to the germ-cells (G) in heredity. (After Wilson.)

germ-cells. Body (or somatic) influences are not inherited. This knowledge we owe largely to Weismann, who showed experimentally that mutilations are not inherited. The tails of mice were cut off for twenty generations in succession, but without effect upon the character of the race. Weismann also pointed out the total lack of evidence for the then current belief that characters acquired by the body are inherited. The correctness of his view that body and germ-cells are physiologically distinct is indicated by the results obtained when germ-cells are transplanted from one individual to another.

Heape showed some twenty years ago that if the fertilized egg of a rabbit of one variety (for example an angora, i. e. a long-haired, white animal) be removed from the oviduct of its mother previous to its attachment to the uterine wall, and be then transferred to the oviduct of a rabbit of a different variety (for example a Belgian hare, which is short-haired and gray), the egg will develop normally in the strange body and will produce an individual with all the characteristics of the real (angora) mother unmodified by those of the foster mother (the Belgian hare). Young thus obtained by Heape were both long-haired and albinos, like the angora mother. To this experiment the objection might be offered that the transplanted egg was already full-grown and fertilized when the transfer was made, and that therefore no modification need be expected, but if the egg were transferred at an earlier stage the result might have been different. In answer to such a possible objection the follow-

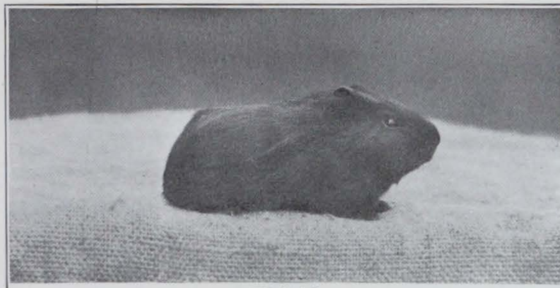

FIG. 10.

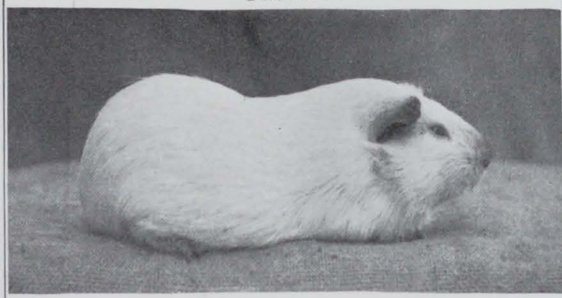

FIG. 11.

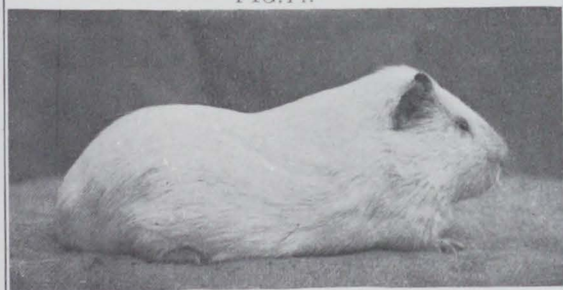

FIG. 12.

FIG. 10. — A young, black guinea-pig, about three weeks old. Ovaries taken from an animal like this were transplanted into the albino shown below.

FIG. 11. — An albino female guinea-pig. Its ovaries were removed, and in their place were introduced ovaries from a young, black guinea-pig, like that one shown in Fig. 10.

FIG. 12. — An albino male guinea-pig, with which was mated the albino shown in Fig. 11.

ing experiment performed by Dr. John C. Phillips and myself may be cited.

A female albino guinea-pig (Fig. 11) just attaining sexual maturity was by an operation deprived of its ovaries, and instead of the removed ovaries there were introduced into her body the ovaries of a young black female guinea-pig (Fig. 10), not yet sexually mature, aged about three weeks. The grafted animal was now mated with a male albino guinea-pig (Fig. 12). From numerous experiments with albino guinea-pigs it may be stated emphatically that normal albinos mated together, without exception, produce only albino young, and the presumption is strong, therefore, that had this female not been operated upon she would have done the same. She produced, however, by the albino male three litters of young, which together consisted of six individuals, all black. (See Fig. 13.) The first litter of young was produced about six months after the operation, the last one about a year. The transplanted ovarian tissue must have remained in its new environment therefore from four to ten months before the eggs attained full growth and were discharged, ample time, it would seem, for the influence of a foreign body upon the inheritance to show itself were such influence possible.

In the light of the three principles now stated, viz. (1) the duplex condition of the zygote, (2) the simplex condition of the gametes, and (3) the distinctness of body and germ-cells, we may proceed to discuss the greatest single discovery ever made in the field of heredity, — Mendel's law.

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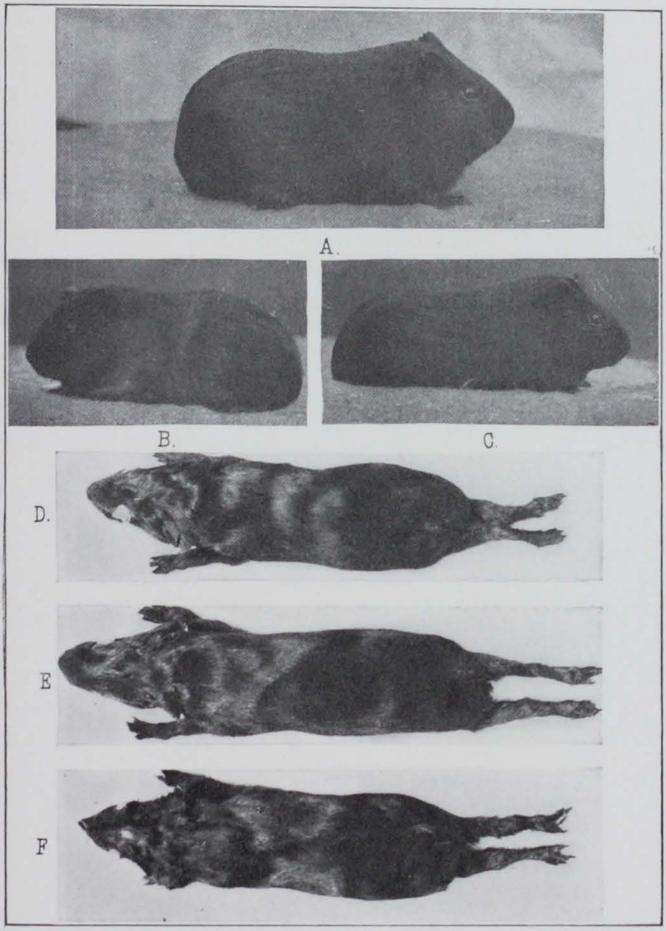

FIG. 13. — Pictures of three living guinea-pigs (*A*, *B*, *C*), and of the preserved skins of three others (*D*, *E*, *F*); all of which were produced by the pair of albinos shown in Figs. 11 and 12.

CHAPTER III

MENDEL'S LAW OF HEREDITY

GREGOR JOHANN MENDEL was a teacher of the physical and natural sciences in a monastic school at Brünn, Austria, in the second half of the last century. He was, therefore, a contemporary of Darwin, but unknown to him as to nearly all the great naturalists of the period. Although not famous in his lifetime, it is clear to us that he possessed an analytical mind of the first order, which enabled him to plan and carry through successfully the most original and instructive series of studies in heredity ever executed. The material which he used was simple. It consisted of garden-peas, which he raised in the garden of the monastery. The conclusions which he reached were likewise simple. He summed them up, the results of eight years of arduous work, in a brief paper published in the proceedings of the local scientific society. There they remained unheeded for thirty-four years, until their author had long been dead. Meantime biological science had made steady progress. It reached the position Mendel had attained in advance of his time, and Mendel's law was rediscovered simultaneously in 1900 by De Vries in Holland, by Correns in Germany, and by Tschermark in Austria. It gratifies our sense of poetic justice that to-day the rediscovered law bears the name, not of any one or of all of its brilliant rediscoverers, but of the all-but-forgotten Mendel.

The essential features of this law can best be explained in connection with some illustrations, which I choose for convenience from my own experiments. If a black guinea-pig of pure race (Fig. 14) be mated with a white one (Fig. 15), the offspring will, as explained on page 10, all be black; none will be white. To use Mendel's terminology, the black character dominates in the cross, while white recedes from view. The black character is, therefore, called the *dominant* character; white, the *recessive* character.

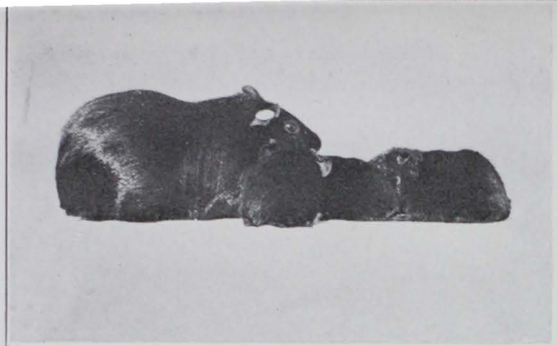

FIG.14.

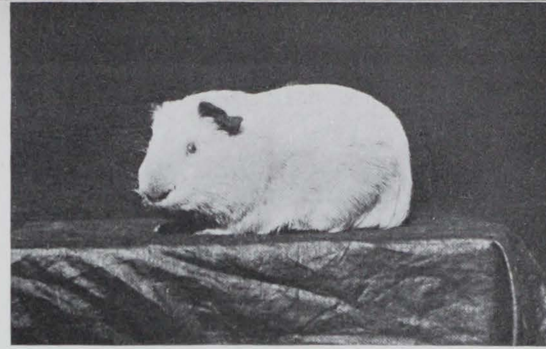

FIG.15.

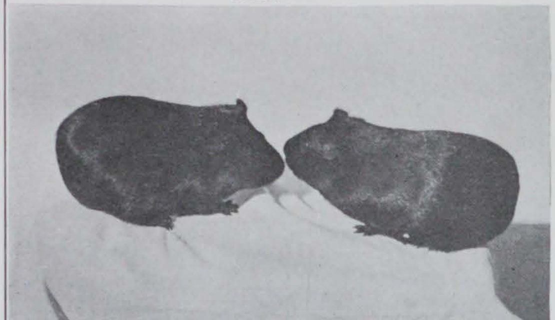

FIG.16.

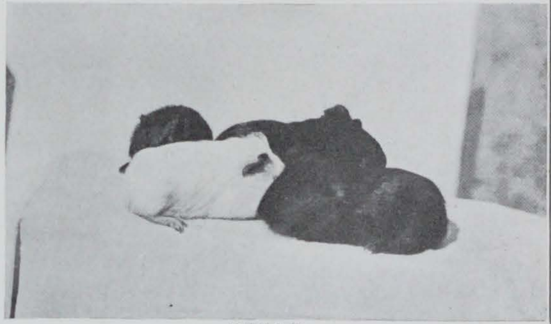

FIG.17.

FIG. 14. — A black, female guinea-pig, and her young.

FIG. 15. — An albino male guinea-pig, father of black young like those shown in Fig. 14.

FIG. 16. — Two of the grown-up young of a black and of an albino guinea-pig. Compare Figs. 14 and 15.

FIG. 17. — A group of four young, produced by the animals shown in Fig. 16.

But, if now two of the cross-bred black individuals (Fig. 16) be mated with each other, the recessive white character reappears on the average in one in four of the offspring (Fig.

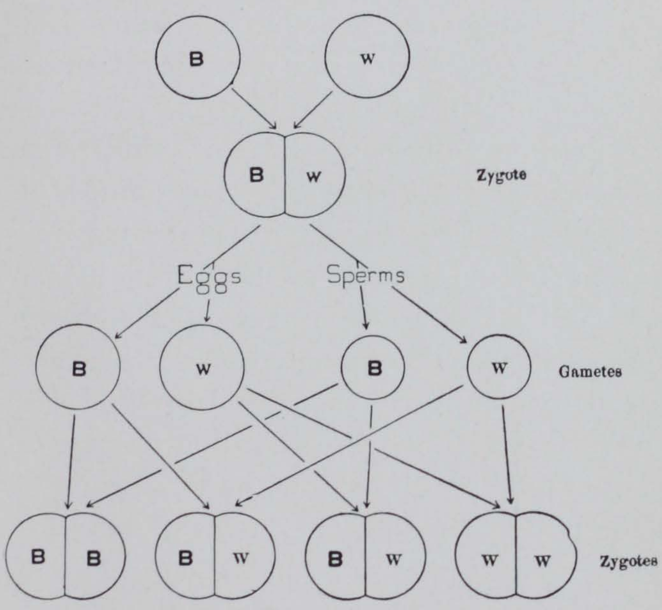

FIG. 18. — Diagram to explain the result shown in Fig. 17.

17). Its reappearance in that particular proportion of the offspring may be explained as follows (see Fig. 18): The gametes which united in the original cross were, one black, the other white in character. Both characters were then asociated together in the offspring; but black from its nature dominated, because white in this case is due merely to the lack of some constituent supplied by the black gamete. But when the cross-bred black individuals on becoming adult form gametes, the black and the white characters separate from each other and pass into different cells, since, as we have seen, gametes are simplex. Accordingly, the eggs formed by a female cross-bred black are half of them black, half of them white in character, and the same is true of the sperms formed by a male cross-bred black. The combinations of egg and sperm which would naturally be produced in fertilization are accordingly 1 B B : 2 B W : 1 W W, or three combinations containing black to one containing only white, which is the ratio of black to white offspring observed in the experiment.

Now the white individual may be expected to transmit only the white character, never the black, because it does not contain that character. Experiment shows this to be true. White guinea-pigs mated with each other produce only white offspring. But the black in-

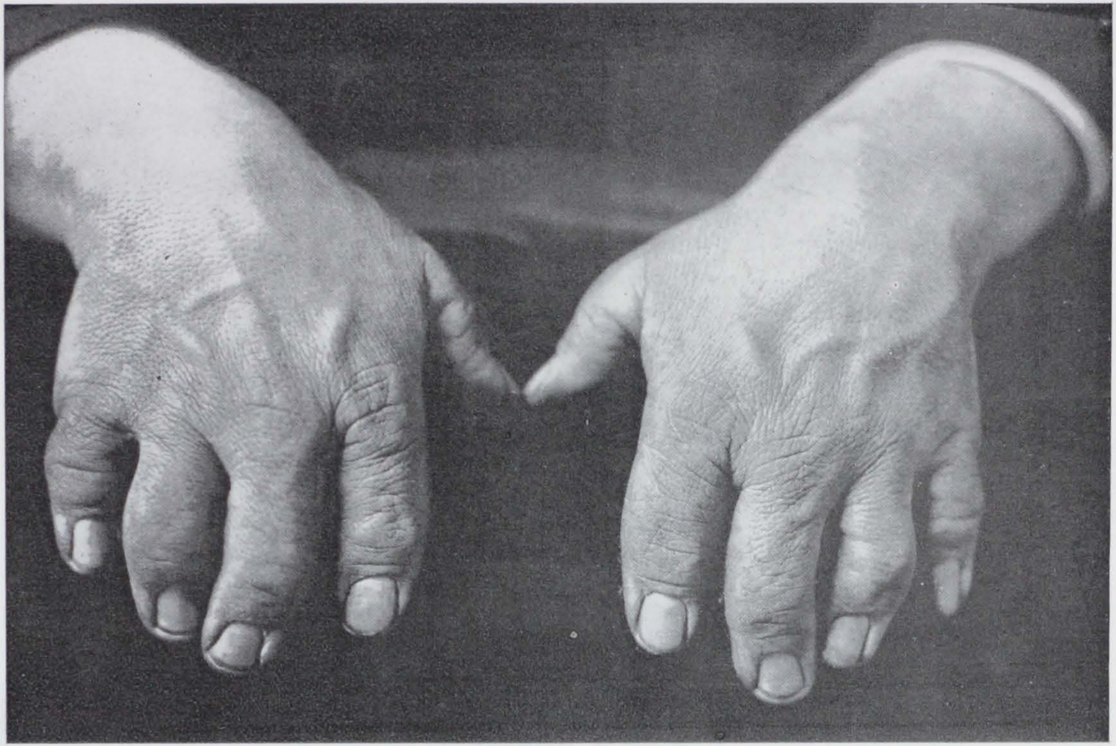

FIG. 19. — A shortened condition of the skeleton, particularly of the fingers, as here shown, is a dominant character in heredity. (After Farabee.)

dividuals of this generation are of two sorts, — B B and B W in character. The B B individual is *pure*, so far as its breeding capacity is concerned. It can form only black (B) gametes. But the B W individuals may be expected to breed exactly like the cross-bred blacks of the previous generation, forming gametes, half of which will carry B, half W. Experiment justifies both these expectations. The test may readily be made by mating the black animals one by one with white ones. The pure (or B B) black individual will produce only black offspring, whereas those not pure, but B W in character, will produce offspring half of which on the average will be black, the other half white. These two kinds of dominant individuals obtained in the second generation from a cross we may for convenience call homozygous and heterozygous, following the convenient terminology of Bateson. A homozygous individual is one in which *like* characters are joined together, as B with B; a heterozygous individual is one in which *unlike* characters are joined together, as B with W. It goes without saying that recessive individuals are always homozygous, as W W for example. For they do not contain the dominant character, otherwise they would show it.

It will be observed that in the cross of black with white guinea-pigs black and white behave as units distinct and indestructible, which may meet in fertilization but separate again at the formation of gametes. Mendel's law as illustrated in this cross includes three principles: (1) The existence of *unit-characters,* (2) *dominance*, in cases where the parents differ in a unit-character, and (3) *segregation* of the units contributed by the respective parents, this segregation being found among the gametes formed by the offspring.

The principles of dominance and segregation apply to the inheritance of many characteristics in animals and plants. Thus in guinea-pigs a rough or rosetted coat (Figs. 23 and 24) is dominant over the ordinary smooth coat. If a pure rough individual is crossed with a smooth one, all the offspring are rough; but in the next generation smooth coat reappears in one fourth of the offspring, as a rule. Again, in guinea-pigs and rabbits a long or angora condition of the

FIG. 20. — Radiograph of a hand similar to those shown in Fig. 19. Notice the short, two-jointed fingers. (After Farabee.)

fur is recessive in crosses with normal short hair. All the immediate offspring of such a cross are short-haired, but in the next generation long hair reappears in approximately one fourth of the offspring.

In cattle, the polled or hornless condition is dominant over the normal horned condition; in man, two-jointed fingers and toes (Figs. 19 and 20) are dominant over normal three-jointed ones. This is clear from an interesting pedigree given by Farabee of the inheritance of the abnormality in a Pennsylvania family (see Fig. 21). In no case was an abnormal member of the family known to have married any but an unrelated normal individual. It will be seen that approximately half the offspring throughout the four generations of offspring shown in the table were of the abnormal sort, — short-bodied and with short fingers and toes.

In each of the cases thus far considered a single unit-character is concerned. Crosses in such cases involve no necessary change in the race, but only the continuance within it of two sharply alternative conditions. But the result is quite different when parents are crossed

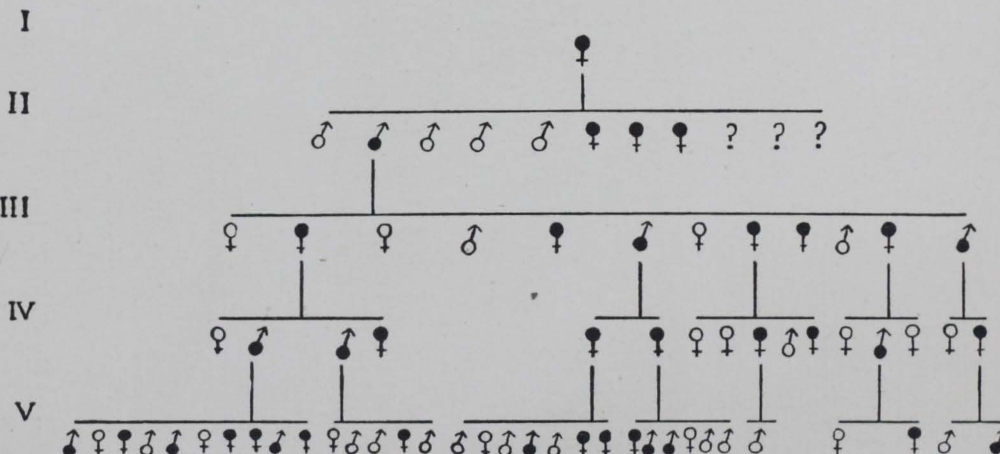

FIG. 21. — Diagram showing the descent, through five generations, of the condition shown in Figs. 19 and 20. Black symbols indicate affected individuals.

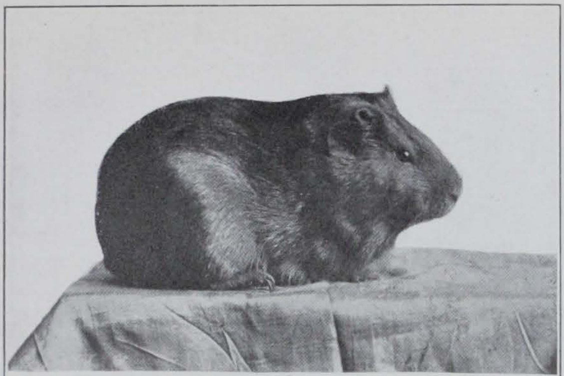

FIG. 22.

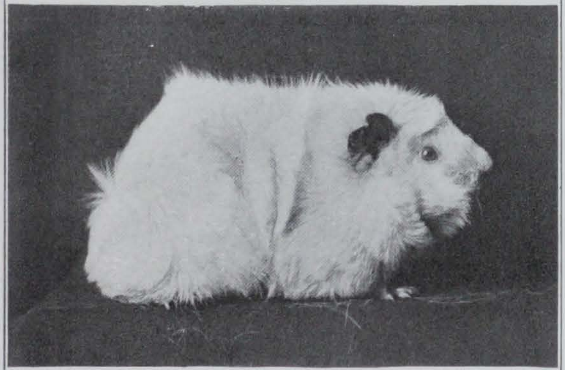

FIG. 23.

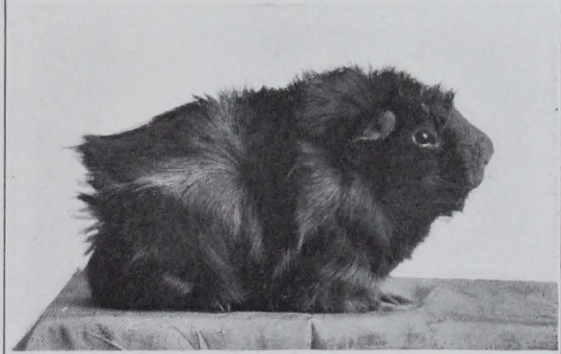

FIG. 24.

FIG. 22. — A smooth, dark guinea-pig.

FIG. 23. — A rough, white guinea-pig.

FIG. 24. — A dark, rough guinea-pig. The new combination of characters obtained when animals are mated like those shown in Figs. 22 and 23.

which differ simultaneously in two or more independent unit-characters. Crossing them becomes an active agency for the production of new varieties.

In discussing the crosses now to be described it will be convenient to refer to the various generations in more precise terms, as Bateson has done. The generation of the animals originally crossed will be called the parental generation (P); the subsequent generations will be called filial generations, viz. the first filial generation (F_1), second filial (F_2), and so on.

When guinea-pigs are crossed of pure races which differ simultaneously in two unit-characters, the F_1 offspring are all alike, but the F_2 offspring are of four sorts. Thus, when a smooth dark animal (Fig. 22) is crossed with a rough white one (Fig. 23) the F_1 offspring are all rough and dark (Fig. 24), manifesting the two dominant unit-characters, — dark coat derived from one parent, rough coat derived from the other. But the F_2 offspring are of four sorts, viz. (1) smooth and dark, like one grandparent, (2) rough and white, like the other grandparent, (3) rough and dark, like the F_1 generation, and (4) smooth and white, a new variety (Fig. 25). It will be seen that the pigmentation of the coat has no relation to its smoothness. The dark animals are either rough or smooth, and so are the white ones. Pigmentation of the coat is evidently a unit-character independent of hair-direction, and as new combinations of these two units the cross has produced two new varieties, — the rough dark and the smooth white.

Again, hair-length is a unit-character independent of hair-color. For if a short-haired dark animal (either self or spotted, Fig. 26) be crossed with a long-haired albino (Fig. 27), the F_1 offspring are all short-haired and dark (Fig. 28); but the F_2 offspring are of four sorts, viz. (1) dark and short-haired, like one grandparent, (2) white and long-haired, like the other, (3) dark and long-haired, a new combination (Fig. 29), and (4) white and short-haired, a second new combination (compare Fig. 25).

Now the four sorts of individuals obtained from such a cross as this will not be equally numerous. As we noticed in connection with

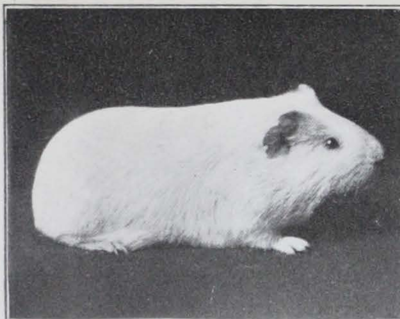

FIG. 25.

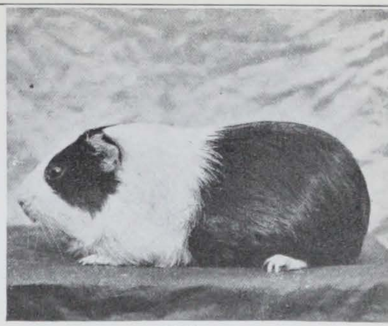

FIG. 26.

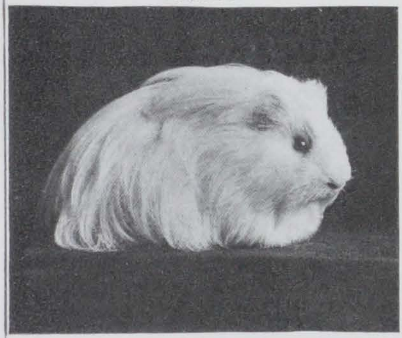

FIG. 27.

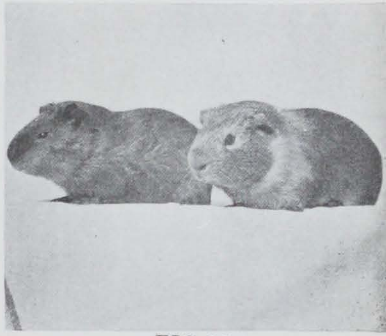

FIG. 28.

FIG. 29.

FIG. 25. — A smooth, white guinea-pig. A second new combination of characters, but obtained first among the *grandchildren* of such animals as are shown in Figs. 22 and 23.

FIG. 26. — A short-haired, pigmented guinea-pig. ("Dutch-marked" with white.)

FIG. 27. — A long-haired, albino guinea-pig.

FIG. 28. — Offspring produced by animals of the sorts shown in Figs. 26 and 27. One shows the "Dutch-marked" pattern as a belt of pale yellow; the other does not. Both are short-haired and pigmented (not albinos).

FIG. 29. — A long-haired, pigmented guinea-pig, "Dutch-marked" with white. Its parents were like the animals shown in Fig. 28; its grandparents like those shown in Figs. 26 and 27.

the black-white cross, dominant individuals are to the corresponding recessives as three to one. Therefore, we shall expect the short-haired in-

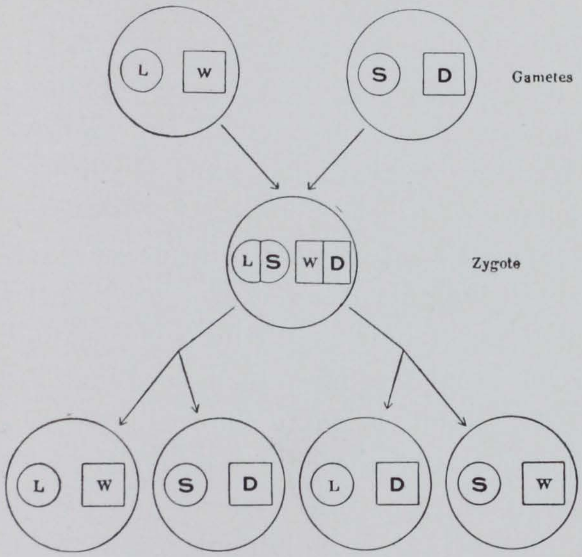

FIG. 30. — Diagram to explain the result of a cross between the sorts of guinea-pigs shown in Figs. 26 and 27. L stands for long hair, S for short hair, D for dark hair, and W for white hair. Dominant characters are indicated by heavy type.

dividuals in F_2 to be three times as numerous as the long-haired ones, and dark ones to be three times as numerous as white ones. Further, individuals which are *both* short-haired and dark should be 3×3 or 9 times as numerous as those which are not. The expected proportions of the four classes of F_2 offspring are accordingly $9:3:3:1$, a proportion which is closely approximated in actual experience. The Mendelian theory of independent unit-characters accounts for this result fully. No other hypothesis has as yet been suggested which can account for it.

Suppose that each unit has a different material basis in the gamete. Let us represent the material basis of hair-length by a circle, that of hair-color by a square, then combinations and recombinations arise as shown in Fig. 30. The composition of the gametes furnished by the parents is shown in the first line of the figure; that of an F_1 individual (or zygote), in the second line; that of the gametes formed by the F_1 individual in the third line. L meets S and W meets D in fertilization to form an F_1 individual double and also heterozygous as regards hair length and hair color, but these units segregate again as the gametes of the F_1 individuals are formed, and it is a matter of chance whether or not they are associated as originally, L with W and S with D, or in a new relationship, L with D and S with W. Hence we expect the F_1 individuals to form four kinds of gametes all equally numerous, — L W, S D, L D, and S W. By chance unions of these in pairs nine kinds of combinations become possible, and their chance frequencies will be as shown in Fig. 31. Four of these combinations, including nine individuals, will show the two dominant characters, short and dark; two classes, including three individuals, will show one dominant and one recessive character, viz. dark and long; two more classes, including three individuals, will show the other dominant and the other recessive character, viz. short and white; and lastly, one class, including a single individual, will show the two recessive characters, long and white. The four *apparent* classes, or, as Johannsen calls them, *phenotypes*, will accordingly be as 9 : 3 : 3 : 1. This is called the normal Mendelian ratio for a dihybrid cross, — that is, a cross involving two unit-character differences.

One individual in each of these four classes will, if mated with an individual like itself, breed true, for it is homozygous, containing only like units. The double recessive class, long white, of course contains *only* homozygous individuals, but in each class which shows a dominant unit, heterozygous individuals outnumber homozygous ones, as 2 : 1 or 8 : 1. Now the breeder who by means of crosses has pro-

Short Dark.	Long Dark.	Short White.	Long White.
1 S D. S D	1 L D. L D	1 S W. S W	1 L W. L W
2 S D. L D	2 L D. L W	2 S W. L W	
2 S D. S W			
4 S D. L W			
9	3	3	1

FIG. 31. — Diagram showing the kinds and relative frequencies of the young to be expected in F_2 from the crossing of animals shown in Figs. 26 and 27.

duced a new type of animal wishes, of course, to " fix " it, — that is, to obtain it in a condition which will breed true. He must, therefore, obtain homozygous individuals. If he is dealing with a combination which contains only recessive characters, this will be easy enough, for such combinations are invariably homozygous. His task will become increasingly difficult the more dominant characters there are included in the combination which he desires to fix.

FIG. 32. — A long-haired, rough albino guinea-pig; male, 2002.

The most direct method for him to follow is to test by suitable matings the unit-character constitution of each individual which shows the desired combination of characters, and to reject all which are not homozygous. In this way a pure race may be built up from individuals proved to be pure. Such a method, however, though sure, is slow in cases where the desired combination includes two or more dominant unit-characters, for it involves the application of a breeding test to many dominant individuals, most of which must then be rejected. It is therefore often better in practice to breed from all individuals which show the desired combination, and eliminate from their offspring merely such individuals as do not show that combination. The race will thus be only gradually purified, but a large stock of it can be built up much more quickly.

We may next discuss a cross in which three unit-character differences exist between the parents, instead of two. If guinea-pigs are crossed which differ simultaneously in three unit-characters, color, length, and direction of the hair, a still larger number of phenotypes is obtained in F_2, namely, eight. A cross betwcen a short-haired, dark, smooth guinea-pig (compare Fig. 22) and one which was long-haired, white, and rough (Fig. 32) produced offspring in F_1 which were short-haired, dark, and rough (compare Fig. 24), these being the three dominant characters, two derived from one parent, one from the other. The F_2 offspring were of eight distinct types, two like the respective grandparents, one like the F_1 individuals (parents), and the other five new, shown in Fig. 33. They are short white rough, short white smooth, long white smooth, long dark rough, and long dark smooth. The largest of the eight apparent classes (phenotypes) was the one which manifested the three dominant characters, short, dark, and rough, which had been the exclusive F_1 type; the smallest class was the one which manifested the three recessive characters, long, white, and smooth. Theoretically these two classes should be to each other as 27 : 1. Of the twenty-seven triple-dominants, twenty-six should be heterozygous.

A comparison of this case with the one just previously described shows what an increas-

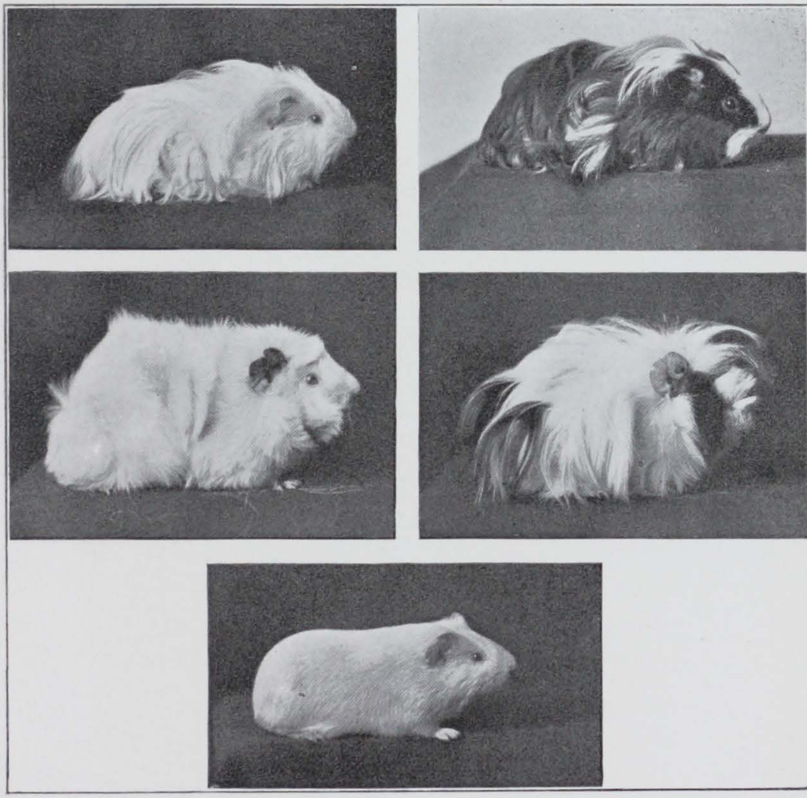

Fig. 33. — Five new combinations of unit-characters obtained in generation F_2, by crossing the animal shown in Fig. 32 with animals like that shown in Fig. 22.

ingly difficult thing it is to fix types obtained by crossing, if the number of dominant characters

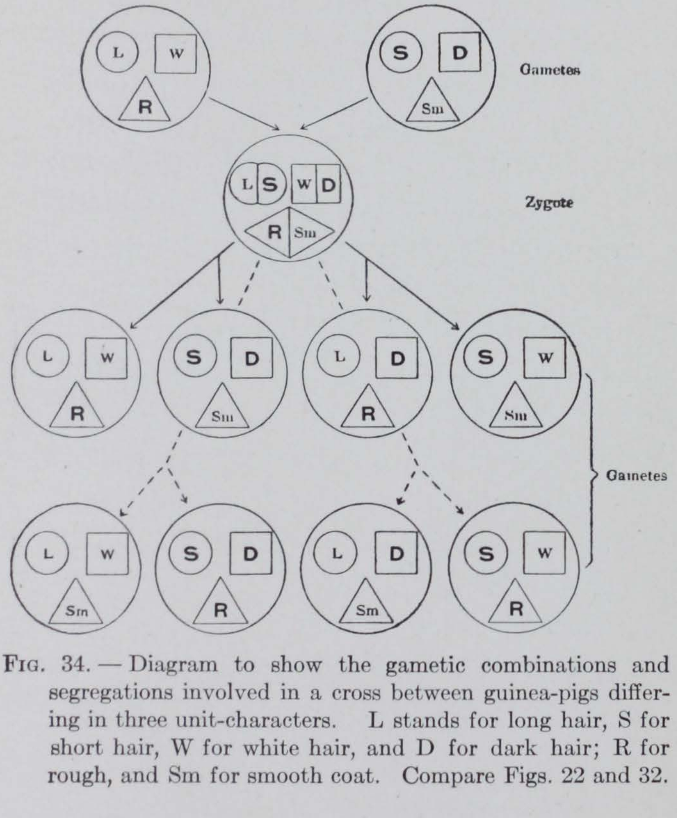

FIG. 34. — Diagram to show the gametic combinations and segregations involved in a cross between guinea-pigs differing in three unit-characters. L stands for long hair, S for short hair, W for white hair, and D for dark hair; R for rough, and Sm for smooth coat. Compare Figs. 22 and 32.

in the selected type increases. On the theory of unit-characters the gametic combinations and segregations involved in this cross are as shown in Fig. 34. The nature of the gametes formed by the parents crossed is shown in the first row; the composition of the F_1 individuals, immediately below. In the two lower rows are shown four different sorts of gametic splittings which may occur in the F_1 individuals, producing thus eight different kinds of gametes. If, in reality, the F_1 individuals form eight kinds of gametes, all equally numerous, and chance unions in pairs occur among them, there should be produced eight corresponding sorts of individuals numerically as 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1. In a total of 64 individuals there should be on the average one pure individual in each of the eight different classes. The class numerically 27 in 64 manifests three dominant characters; those which are numerically 9 in 64 manifest two dominant characters; those which are numerically 3 in 64 manifest one dominant character. Among each of these there will be on the average one pure individual, but the class which contains 1 individual in 64 is a pure recessive, for it contains no dominant character. This combination, then, requires no fixation. It will breed true from the start.

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