XI

HOW DARWINISM STANDS TO-DAY

VARIATION—SELECTION—HEREDITY—MENDELISM

WHEN people speak of Darwinism they sometimes mean the general idea of evolution—that the present is the child of the past and the parent of the future. Now the evolutionary way of looking at things has certainly been confirmed by the progress of science and is almost unanimously accepted by competent judges to-day. This horse that gallops past on the tiptoe of one digit on each foot is the natural outcome of an ancestral stock of small-hoofed mammals that used to plod about in the Eocene meadows, with four toes on each fore-foot and three and a vestige on each hind-foot. This bird that flies past is the descendant of such an old-fashioned type as the Jurassic Archæopteryx—an archaic bird with teeth in both jaws, a long tail like a lizard's, and a sort of half-made wing. And this first-known bird must be traced back to an ancestry among the extinct Dinosaur reptiles, though the precise pedigree remains hidden in the rocks. These reptiles must be traced back to certain primitive amphibians, and these to certain old-fashioned fishes, and so on, back and back, till we lose our clue in the thick mist of life's beginnings. If this is Darwinism it stands more firmly than ever, except that we are more keenly aware than in Darwin's day of our ignorance as to the origin and affiliation of the great classes. But, frankly, the only scientific way of looking at the present-day fauna and flora is to regard them as the outcome of a natural evolution. In a previous chapter this statement has been justified.

Universal Acceptance of the Evolution Idea.

Photo: Becker and Maas.

PROFESSOR WILLIAM BATESON, F.R.S.

One of the most distinguished of the experimental evolutionists, he has made fundamental contributions to our knowledge of Mendelian heredity and of variation. He has confirmed Mendel's theory and added important elaborations. He has shown that discontinuous variation or mutation is of frequent occurrence. He was President of the British Association on its visit to Australia in 1914.

The Factors in Evolution.

But "Darwinism" is more properly used, in a stricter sense, to mean Darwin's theory of the factors in evolution. If birds sprang from Dinosaur reptiles, if the modern horse is the descendant of Eohippus, which was about the size of a fox-terrier, how did the gradual transformation come about? There were many evolutionists before Darwin, and some of them propounded theories as to the factors in the age-long process. But Charles Darwin and his magnanimous fellow-worker, Alfred Russel Wallace, thought out a coherent theory of the factors—a theory that fitted the facts so reasonably well that it soon won the conviction of a large body of naturalists. The essence of the Darwinian theory is in the two words Variation and Selection; and Darwin stated it in a couple of sentences: "As many more individuals of each species are born than can possibly survive, and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected. From the strong principle of inheritance any selected variety will tend to propagate its new and modified form."

This is, however, too terse a statement. It requires some disentangling and expansion. *Proposition I.*—Variability is a fact of life. Offspring are usually somewhat different from their parents and from the other members of the family. Some of these variations make for success—success in getting food, in avoiding enemies, in securing mates, in giving the next generation a good start, and in other ways. Individuals that have varied in a profitable way will succeed better than those that have varied in the opposite direction, and better than those that have not varied at all.

The Essence of Darwinism.

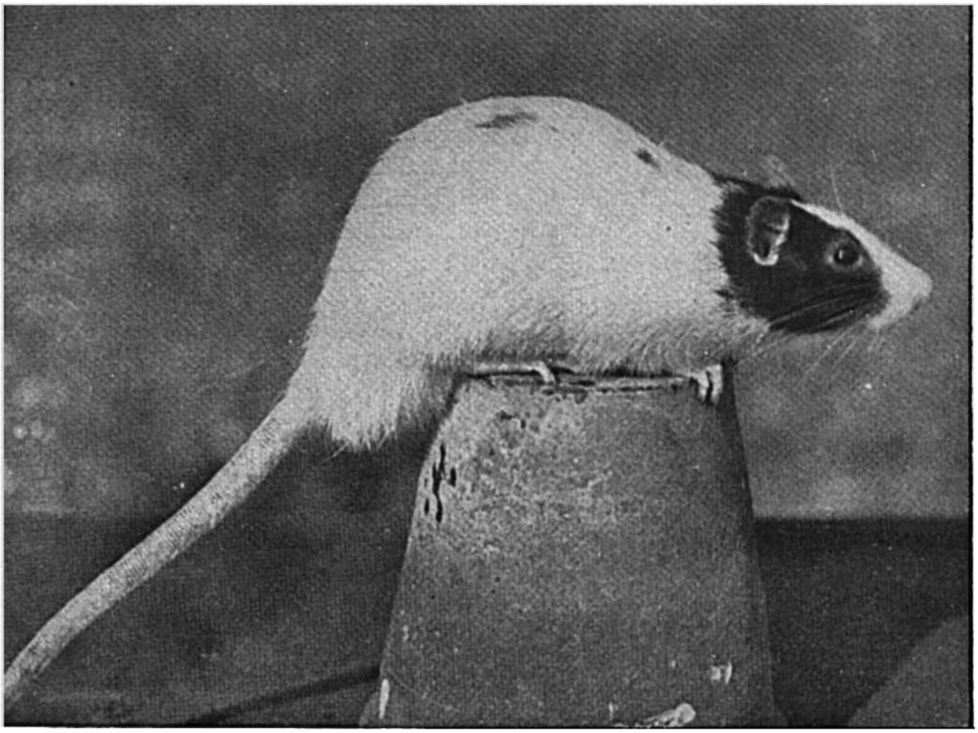
Proposition II.—If the individuals that have varied profitably get the reward of their superiority, and if the individuals that have varied unprofitably, or not at all, are handicapped by their inferiority, this will have an effect on the character of the stock, or race, or species, *provided* that the novel peculiarities are hereditarily entailed on successive generations. If the individuals with profitable peculiarities (let us say, *plus* variants) are consistently favoured, and if their virtues are consistently handed on, their type will come to be that of the race. Whereas those with unprofitable peculiarities or none at all (let us say, *minus* variants) will be weeded out and will gradually disappear. Professor R. C. Punnett has calculated that, "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."

Proposition III.—But there cannot be sifting or selection without a sieve, and that is to be found in the struggle for existence. Living creatures are hemmed in by limitations and confronted by ever-changing difficulties. There is a tendency to over-population; circumstances are changeful; the vigorous creature is a hustler. There is struggle for food, for foothold, for self-preservation, for mates and for family well-being—indeed, for luxuries as well as for necessaries. There is struggle between fellows of the same kind, for a hungry locust may devour its neighbour and even the Amœba may be a cannibal. There is a struggle between foes of quite different kinds, between the grazing herd and the marauding carnivores, between the kestrel hawk and the nimble field-voles. There is struggle also between living creatures and their inanimate surroundings, the struggle against cold and heat, against wind and wave, against drought and flood. Subtle beyond description and almost ceaseless in its operation is nature's sifting, which Darwin called Natural Selection. In domestication and cultivation it is Man who fosters and eliminates; in nature the same kind of transformation as the breeder and the gardener effect is brought about by the struggle for existence.

These three propositions express the gist of Darwinism, and the question before us is, *How Darwinism stands to-day.* Before trying to answer this difficult question, we may point out that it would be a sorry business if Darwinism stood to-day as it was left by Darwin. He knew well that he had only begun to solve the problem of organic evolution; he looked forward with clear eyes to changes that the progress of science would enforce. It would be a terrible contradiction in terms if an evolution theory did not itself evolve! The marvel is, not that it is necessary to make some changes in what Alfred Russel Wallace so generously called "Darwinism," but rather that so much of Darwin's doctrine stands firm, four-square to the winds.

Darwinism in Process of Evolution.

Another preliminary note is unfortunately necessary, that it is quite illegitimate to infer from our dubiety in regard to the *factors* of



A RAT-BREEDER'S TRIUMPH.

A "Dutch-marked" cross between a black and a white rat, bred by Mr. H. C. Brooke. It shows a probably unique symmetry of markings. The black and white rats of the fancier are both derived from the common brown rat (*Rattus norvegicus*) and have nothing to do with the wild black rat (*Rattus rattus*).

evolution any hesitation as to the *fact*. Our frankness in admitting difficulties and relative ignorance in regard to the variations and selections that led from certain Dinosaurs to Birds cannot be used by any fair-minded inquirer as an argument against the idea of evolution. For how else could Birds have arisen? As Wallace said in 1888, "Descent with modification is now universally accepted as the order of nature in the organic world." But the question before us is this: What, as regards the factors in evolution, have been the changes since Darwin's day?

§ 1

The Three Problems of Evolution.

There are three great problems before the evolutionist: (1) What is the origin of the new? (2) What are the laws of inheritance? (3) What are the sifting methods that operate on the raw materials provided and determine survival? In other words: what are the originative factors, what are the laws of entail, and what are the directive or sifting factors?

Evolution depends on new departures, peculiarities, idiosyncrasies, divergences, freaks, sports, a little more of this, a little less of that—in short, organic or constitutional changes. These are technically called variations and mutations. In other words, evolution—whether progressive or retrogressive—depends on the emergence of novelties. When there are no novelties there can be no evolution. The Lamp-shell, Lingula, seems to have remained stagnant for many millions of years—a fine creature, but icily perfect.

Heredity is the relation of organic continuity between successive generations, the living on of the past in the present, the flesh and blood linkage between an individual and his forbears on the one hand, his offspring on the other. The individual is like a lens into which rays from parentage and ancestry converge, from which they diverge again to the progeny.

Heredity is the reproductive relation which secures that like *tends* to beget like, and yet seldom does. Some peculiarities of an individual are heritable, others are not; longevity is readily entailed, but genius is not; deaf-mutism is very transmissible, but a very brown Anglo-Indian father has a peach-blossom complexioned daughter. Thus, if we think clearly, we see that heredity is not so much a factor in evolution as a *condition*. There would still be heredity though evolution stopped; but there can be no evolution without heredity. For heredity implies that the gains of the past can be capitalised; and, contrariwise, that individual losses need not involve racial bankruptcy. A man who has lost an eye may be assured that his son will have two, even if the mother is single-eyed as well.

What are called variations and mutations in biological language are the organism's experiment in self-expression, and these are the raw materials of progress. Granted raw materials, and granted their continuance, something more is needed—their sifting. As we have said in a previous article, the process of evolution is a long drawn-out process of testing all things and holding fast that which is good. The variations or novelties are the qualities to be tested; the struggle for existence, which includes the organism's endeavours, is the sieve that tests; *heredity secures the holding fast of what has proved good.* To employ a metaphor which has the defect of triviality, the variations are the ever-fresh hands of heredity cards that are given to the organism to play with; the organism uses these in the struggle for existence—with its strange mixture of active endeavour and fortuity. But when the organism with a good hand—a persistently good hand—becomes eventually tired and vacates its chair for a successor, it hands on its luck, and its cunning too. Thus the essence of Darwinism is that nothing succeeds like success.

§ 2

As regards Variations.

The fountain of change is even more copious than Darwin supposed. What is so clear in regard to pigeons and poultry, dogs and horses, that they are continually producing something new in their humanly controlled breeding, finds abundant illustration in wild nature. There are conservative types, it is true, which persist in a well-poised organic equilibrium, but in many cases there is flux. Outlying variants link one species to another. When the novelties or variations are registered statistically they often form what is called the Curve of Frequency of Error, which means that the number of variants of any particular magnitude will be in inverse proportion to the amount of the deviation from the mean. If the mean stature of the population be 5 ft. 8 in., there will be (as Alfred Russel Wallace points out) in 2,600 men, taken at random, one of 4 ft. 8 in. and one of 6 ft. 8 in., twelve of 5 feet, and about twelve of 6 ft. 4 in. In fact, there will be equal numbers at equal distances on each side of the mean, but the great majority of the deviations will be not far from the mean.

Definiteness in Variation.

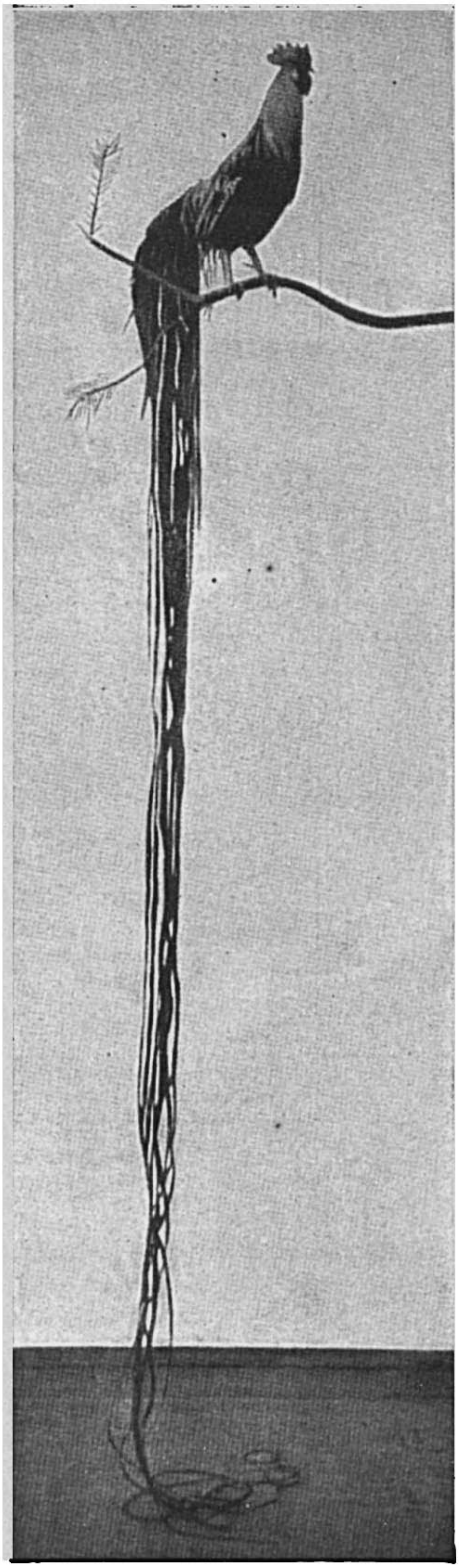
Since Darwin's time evidence has accumulated which shows that variations are more definite than used to be supposed. The palæontologists, who work out long series of fossils, bring forward cases of what looks like steady progress in a definite direction. There is a striking absence of what one might call arrows shot at a venture. It looks as if the occurrence of the new were limited by what has gone before, just as the architecture of a building that has been erected determines in some measure the style of any addition. An organic new departure will tend to be more or less congruent with what has been previously established. In post-Darwinian days the element of the fortuitous has shrunk.

Discontinuous Variations.

Darwin was much interested in sports or freaks, such as the sudden appearance of a dwarf or a giant, a hornless calf or a tailless kitten, a white blackbird or a weeping ash, a thornless rose or a stoneless plum, a "wonder-horse" with its mane reaching the ground, or a Japanese cock with a tail six feet long. But Darwin did not venture to attach great importance to these brusque novelties, or discontinuous variations, first because he thought they were of rare occurrence, and second because he thought they would be speedily averaged off in the offspring of a sport which had paired with an ordinary individual. He did not know what his contemporary Mendel proved, that when a pure-bred tall pea and a pure-bred dwarf pea are crossed the offspring are all *tall*.

Now one of the great changes that has come about since Darwin's day is a recognition of the frequency of discontinuous variations, by which we mean sudden novelties which are not connected with the type of the species by intermediate gradations. We may think of the white crow or the weeping willow. The Proteus leaps as well as creeps. Especially through the investigations of Professor William Bateson and Professor Hugo de Vries, it has become plain that changes of considerable magnitude may occur at a bound. When the new character that suddenly appears, such as a Shirley Poppy or a short-legged Ancon Sheep, has a considerable degree of perfection from its first appearance, is independently heritable to the offspring, and does not blend or average off, it is called a *Mutation*. Professor de Vries writes: "The current belief assumes that species are slowly changed into new types. In contradiction to this conception the theory of mutation assumes that new species and varieties are produced from existing forms by sudden leaps. The parent type itself remains unchanged throughout the process, and may repeatedly give birth to new forms. These may arise simultaneously and in groups, or separately, at more or less widely distant periods." This was strikingly illustrated by the sporting Evening Primrose (*Œnothera lamarckiana*), a species of North American origin, which de Vries found at Hilversum in Holland, and which proved to be in a very changeful mood. Almost all its organs were varying, as if swayed by a restless internal tide. It gave rise abruptly to numerous new forms which bred true. It illustrated species in the making.

Darwin found the raw material of evolution in small fluctuating variations, which are no doubt of frequent occurrence. Since Darwin's day it has become not only possible but necessary to attach much importance to discontinuous mutations. The contrast was aptly illustrated by Sir Francis Galton, who compared the varying organism to a polyhedron (a solid body with many faces) which can roll from one face to another. When it settles down on any particular face it is in stable equilibrium. Small disturbances may make the polyhedron oscillate, but it always returns to the same face.



JAPANESE LONG-TAILED FOWL OR TOSA FOWL.

In this extraordinary breed, which is believed to be of very ancient origin, the feathers of the tail show continuous growth, reaching 7 to 8 feet, and in extreme cases 18 feet. This seems to be a physiological mutation. The offspring of a cross between a Tosa cock and a white cochin Bantam hen yielded males with the Tosa coloration except that every feather was barred with white. The males had abnormally long middle tail-feathers, but not so long as in the Tosa cock. The female offspring were like Tosa hens.

These oscillations are like Darwin's fluctuating variations, but the comparison breaks down inasmuch as the living creature may be, as it were, fixed in one of its oscillations, so that the variant makes a fresh start. Greater disturbances of the polyhedron may make it roll over on to a new face altogether, where it comes to rest again, only showing once more the minor fluctuations around its new centre. The new position corresponds to what is now called a mutation. Studies in inheritance have shown that these mutations have great staying power; they reappear persistently and intactly in a certain proportion of the descendants. They are not liable to be swamped by intercrossing, as Darwin supposed. The curious fact is that the hereditary entailment of the fluctuating variations, which Darwin almost took for granted, requires more demonstration to-day than does the hereditary entailment of mutations.

Photo: Rischgitz Collection.

GREGOR MENDEL, ONE OF THE FOUNDERS OF THE SCIENTIFIC STUDY OF HEREDITY.

Gregor Johann Mendel (1822–84), the son of well-to-do peasants in Silesia, became a priest in 1847, studied physics and natural science at Vienna from 1851 to 1853, eventually became Abbot of Brünn. In the garden of the monastery he made experiments with peas, hawkweeds, and bees; and published in 1865 what must be regarded as one of the greatest of biological discoveries. It was practically lost sight of till 1900. Regarding "Mendel's Law," Professor Bateson says: "The experiments which led to this advance in knowledge are worthy to rank with those that laid the foundation of the atomic laws of chemistry."

§ 3

Variations and Modifications.

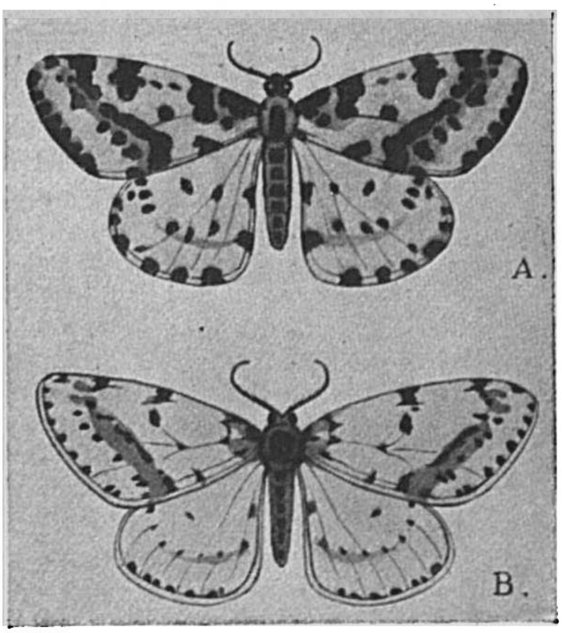
Under the influence of persistent exercise, such as dancing, the muscles of the legs increase in size, and the tendency to increase may spread in an interesting way to other parts of the body. Long-continued exercise of white rats increases the weight of the heart, kidneys, and liver, on an average about 20 per cent. Water-snails reared in cramped surroundings grow up dwarfish. Goldfishes kept in the dark for three years become totally blind. If the wan pigmentless Proteus from the Dalmatian caves be exposed to light it becomes black, and the eggs laid by individuals kept in the light develop into dark larvæ. Prolonged pressure on a particular part of the skin often produces a thickening or callosity. The colours of birds' feathers are sometimes affected by the food they eat, as is well known in the case of canaries and parrots. The stomach of the herring-gull changes its character according to the diet—whether it be fish or grain.

Now all these changes are technically called "modifications"; they are directly induced *in the individual lifetime* by peculiarities in habits and surroundings, including food. They are also called "acquired characters"—a very unfortunate term. *They are impressed from without*, whereas true variations and mutations *are expressed from within.*

Modifications are indents or imprints, variations are outcomes. According to the evolution theory of Lamarck, which Darwin accepted in some measure, the characters of a race may slowly change through the cumulative inheritance of the modifications which individuals acquire as the result of peculiarities in use and disuse, and in surroundings. A cave animal is blind, according to Lamarck, as the result of ages of living in darkness, during which the eyes have suffered from disuse. The modern

Darwinian would point to the fact that constitutional or germinal variations in eyes are common. Variants with weak eyes and with a bias in that direction would naturally seek out caves. The giraffe has got a very long straight neck because of the cumulative result of generation after generation of stretching up to the branches of the acacia-trees. With certain provisos Darwin inclined to accept this view as supplementary to his own. But the modern Darwinian would point to the fact that constitutional or germinal variations in the proportions of different parts of the body are common. Giraffe variants in the direction of a long neck would prosper, and would become the leaders of the race. Long noses often run in families, but the length of the nose is not due to the vigour with which generations have used the handkerchief.

No one doubts the reality of modifications: one has only to look at the tanned skin of the African explorer. But what is doubtful is that a modification can be passed on from the individual that acquires it to his offspring—passed on as such or in any representative degree. The modification may be very important, even life-saving, for the individual, but unless it can be transmitted it is not in any direct way important for the race. The scepticism as to transmission of bodily modifications was focussed by Sir Francis Galton and by Professor August Weismann; and many would say that one of the great changes in Darwinism since Darwin's day has been the abandonment of belief in the Lamarckian postulate of the transmission of modifications. There are some difficult cases, however, which suggest that biologists must not be in a hurry to shut out the possibility of such transmission. Admitting a few difficult cases, we can only record our impression that the available evidence indicating a transmission of "acquired characters" as such or in any representative degree is very inconclusive. But this would not be admitted by such a distinguished zoologist as Professor E. W. MacBride; and the scientific outlook should be that of an open mind, associated with an eager search for more facts.



VARIATION IN THE MAGPIE MOTH.

This common moth, *Abraxas grossulariata*, which ranges from Britain to Japan, and is famous for its extraordinary number of variations in colour and markings. Such slight differences as those between the type A and the variety B (*lacticolor*) illustrate the minute variations which form part of the raw material of evolution.

Those who are unfamiliar with the subject often ask how a race could make progress at all if acquired characters were not transmitted from generation to generation. The answer is that the changes which make for racial progress are variations and mutations—*arising from within*, from disturbances and rearrangements, permutations and combinations, in the germ-cells from which new individuals arise. In 1796 the utmost speed of the trotting horse was stated at a mile in 2 min. 37 sec.; in 1896 at 2 min. 10 sec. Does it not follow that the trotting horse has been improved by the transmission of the results of the systematic training in trotting? It is certain that this conclusion does not follow from the available evidence, which points to the conclusion that the improvement in speed has been mainly due to the selective breeding of constitutionally swift horses. The trotter is born, not made.

It should also be understood that modifications may reappear, *not because* they have been transmitted, but because the conditions which originally brought about the change may still persist and produce the same effect on the offspring. And as to the inheritance of disease, this is apparently confined to constitutional diseases which are due to disturbances in the germ-cells. Diseases due to peculiarities of occupation or diet are not transmitted as such, though an unborn offspring may be poisoned before birth, or even infected with some disease microbe.

Another common misunderstanding must be cleared up, namely, the idea that if peculiarities directly induced by improvements in human "nurture" (surroundings, food, and habits) are not handed on to the offspring, then such improvements are not of great importance. But if the beneficial results of improved function and environment are not as such transmitted, it becomes all the more urgent that they should be reimpressed on each successive generation. If they are not entailed, then it is all the more important that they should be *re-acquired*. Moreover, these ameliorations of "nurture" (in the wide sense) may serve as the liberating stimuli that encourage the unfolding of new variations of a useful sort. Besides, it has to be borne in mind that, although the direct effects of fresh air, exercise, good food, beautiful surroundings, pleasant work, and the like, may not be transmitted as such or in any representative degree, they may increase the general vigour of the next generation, and will certainly do so when the mother influences the offspring before birth—an influence which is not in the strict sense part of the inheritance. Given a constitutional taint or weakness, it may be counteracted by suitable "nurture," but that will not make it disappear from the inheritance. It will crop up in a later generation if it gets a chance. In breeding animals and cultivating plants there seems to be no use working with individuals showing advantageous *modifications*; the only hope is to select from among advantageous *variations* or *mutations*. Finally, it should be noted that if advantageous modifications are not entailed, which may be a matter for regret, the same non-transmission will hold in regard to disadvantageous modifications, whereat we may congratulate ourselves.

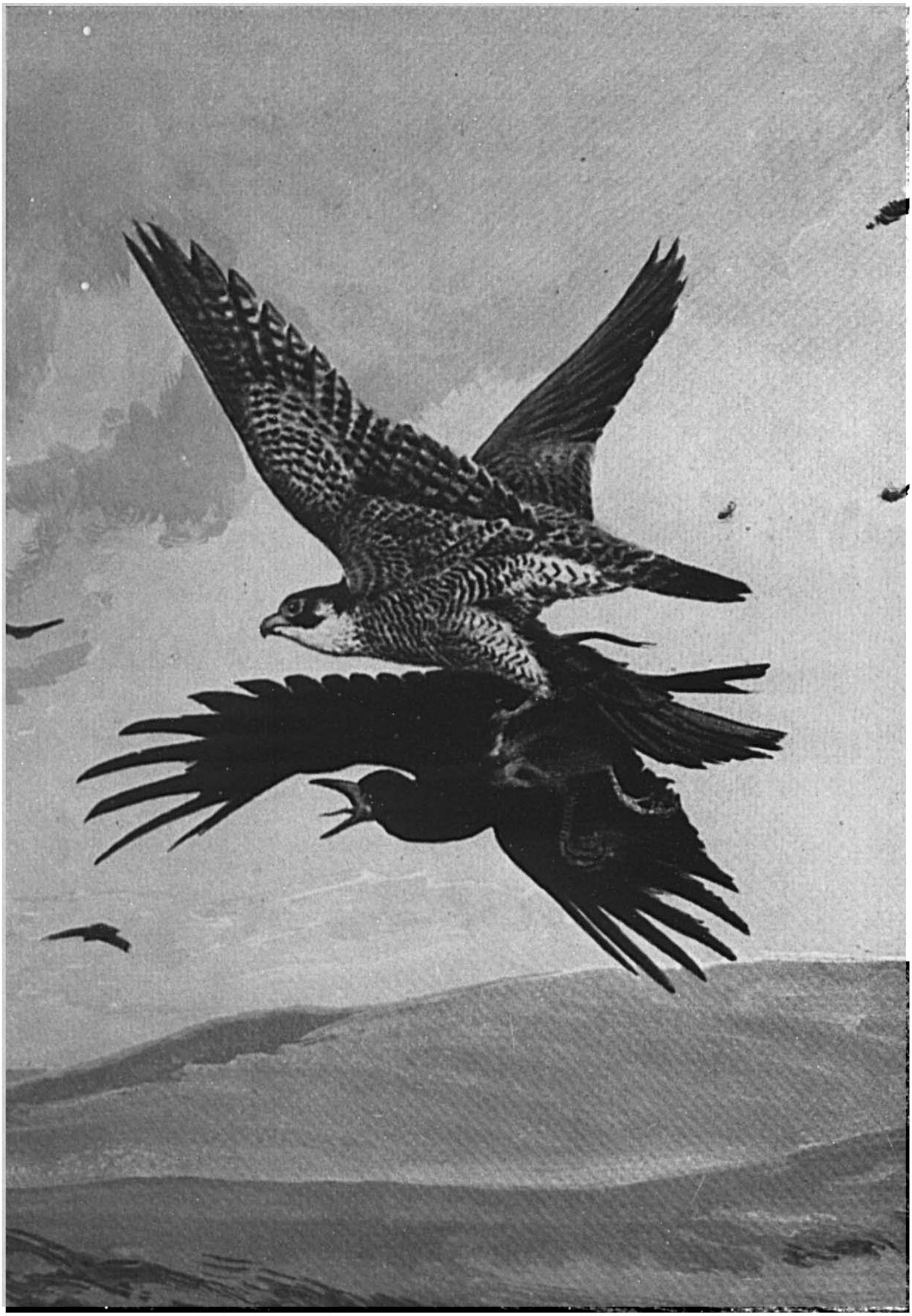
§ 4

Darwin had no theory of the origin of variations, and we must join with him in saying "our ignorance of the laws of variation is profound." This is the central problem of evolution—the origin of the new. Yet certain possibilities have become clearer since Darwin's day. When a white blackbird is hatched, when an albino child is born, when a calf appears without horns or a kitten without a tail, we interpret these variations as due to the dropping out of the relevant hereditary item in the inheritance, and we know that in the history of the germ-cells there are definite opportunities for such losses.

Origin of Variations.

When, on the other hand, an offspring has more than usual of a certain character we can interpret this as due to its getting a double dose—from both sides of the house—of the hereditary item in question. If both parents are very dark and come of very dark stocks, the offspring may be darker still, and the same holds terribly true of a double dose of some disadvantageous character, such as deaf-mutism. The individual life always begins in the fertilised egg-cell, and there may be accentuation of a character, we say, if it is strongly represented both in the paternal and in the maternal hereditary contributions. In the sperm-cell as in the egg-cell there is a complete set of hereditary "factors" or initiatives, and these two sets come into intimate and orderly union in fertilisation. When the fertilised egg develops into an embryo and into a young creature, there may be an expression of some paternal peculiarities and some maternal peculiarities, with a new pattern as the result. It must be understood that although there is a complete assortment of hereditary qualities in the egg-cell and also in the sperm-cell, it is usually only one set that finds expression in the offspring in regard to any particular structure. The child may have its mother's hair, its father's chin. In some cases a father's character as regards some particular feature is seen only in his sons, not in his daughters. But the feature may appear in his daughter's sons.

When the human variant shows a new pattern of a particularly happy kind, we call it "genius"; when the outcome is more dubious we say "crank". And the animal kingdom is full of geniuses and cranks. Our point, however, is just this, that fertilisation offers an opportunity for new permutations and combinations. If we may compare an inheritance to a pack of cards, each hereditary constituent or "factor"



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A FACTOR IN THE STRUGGLE FOR EXISTENCE (PEREGRINE FALCON ATTACKING A ROOK)

The Peregrine Falcon, which has been described as "the most powerful bird for its bulk that flies," preys largely on other birds, which it attacks during flight. The Falcon's aim is always to get higher than its quarry; it then "stoops" from above, killing not by force of impact but by the grip of its strong talons. As in many birds of prey, the female is larger and stronger than her mate and can hunt larger game.

corresponding to a card, then there is in fertilisation a re-shuffling, just as there is in the maturation of the germ-cells an opportunity for cards being lost. We may say, then, that an increased knowledge of the history of the germ-cells since Darwin's day has made it possible to understand how certain kinds of variations may arise.

If we probe a little deeper, we see the possibility that the stimuli of outside changes, e.g. of climate, may saturate through the organism *and provoke the complex germ-cells to change.* Thus Professor W. L. Tower subjected potato-beetles at a certain stage of their development to very unusual conditions of temperature and humidity. The beetles themselves were not changed, for these hard-shelled creatures do not lend themselves to external modification. But in a number of cases the *offspring* of the beetles showed remarkable changes, e.g. in colour and markings. And the offspring of these variants did not revert to the grandparental type. In such a case it looks as if an environmental stimulus penetrating through the body serves as the liberator or stimulus of variability in the germ-cells.

It may seem for a moment that this case of the potato-beetles indicates the inheritance of the results of environmental influence. But it must be carefully noticed that the parent beetles showed no modification or acquired character. What happened was that a peculiarity of environment saturated through the body, and started a germinal peculiarity, which all biologists are agreed in regarding as heritable. Similarly, persistent alcoholism on the part of a strong parent may prejudice the offspring by provoking disturbance in the germ-cells. But this is very different from the transmission of hardened liver or any other specific modification. Everyone knows that alcoholism of parents does not make for vigorous progeny, but it must be insisted that this does not bear very directly on the technical problem of the transmission of modification. In most cases what is inherited in the alcoholic lineage (rarely a long one) is a constitutional defect, e.g. lack of control. In some cases the parental intemperance affects the germ-cells prejudicially ; though in some animals the results of experiments do not corroborate this. It seems to vary with the organism. Finally, the offspring of an alcoholic mother may be badly handicapped before birth, but this has as little bearing on the transmission of acquired characters as the fact that whisky babies do not thrive. It is not legitimate to re-define "acquired characters" ; the term means—modifications of structure acquired in the individual lifetime as the direct result of peculiarities in surroundings, food, and function.

Professor Weismann laid emphasis on the somewhat subtle idea that the complex germ-plasm, which somehow contains the whole inheritance, might be prompted to vary by fluctuations in the nutritive stream of the body. Just as poisons in the blood may deteriorate the germ-cells in definite ways, so the gentler influence of slight changes in nutrition may induce the germ-cell to internal re-arrangements which are by and by expressed as profitable variations. It should not be forgotten that differences in diet determine whether the grub of a bee is to develop into a worker or into a queen.

It seems fair to say that the problem of the origin of variations is not so dark as it was in Darwin's time. At the same time no one can pretend to understand the emergence of the distinctively new. The germ-cell is a living creature in a single-cell phase of being, and it may be that its variations are the outcomes of a primary quality of living creatures, inherent in the germ-cell—the capacity of making experiments in self-expression.

§ 5

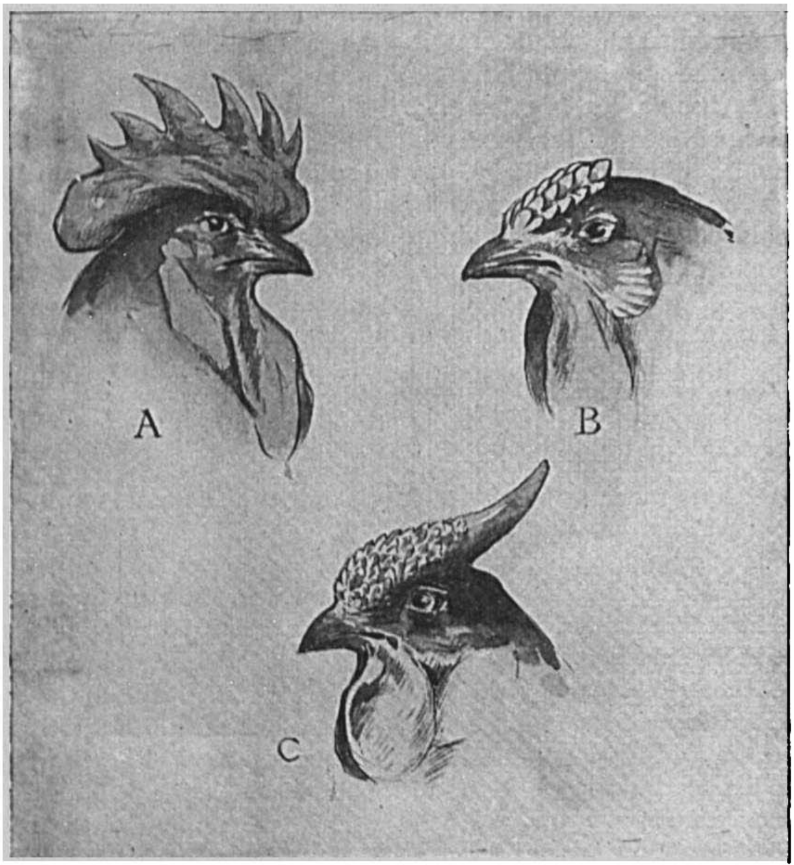
As regards Heredity.

Darwin was one of the first to show that the mysterious problems of heredity could be attacked scientifically, and his cousin Sir Francis Galton went much further. But it is unfortunate that neither of them knew anything about the Abbé Mendel, who published papers in 1865 which have revolutionised the whole subject. His work remained practically unknown till 1900.

Mendelism.

There are three fundamental ideas in Mendelism. The *first* is the idea of "unit-characters," and this requires a little patience. By an inheritance is meant what the living creature is or has to start with, when it is represented by a fertilised egg-cell. Now it has been discovered that an inheritance is, in part, built up of numerous, more or less clear-cut, crisply defined, non-blending characters, which are continued in some of the descendants as definite wholes, neither merging nor dividing. We may think of the colour of the eye, the quality of the hair, the shape of the nose. Strictly speaking, what lies in the inheritance is not the character as seen in the adult but a germinal representative (technically called a "factor" or "gene") of the character. The full-grown character, say the shape of the nose, is, as it were, *a product of the germinal representative and the surrounding influences which operate during development.* It is also necessary to understand that an adult character, like the quality of the hair, may be represented in the germ-cell by several factors. Moreover, one germinal factor, e.g. the initiative for developing dark pigment, may influence several characters in the adult.

If a man has his fingers all thumbs, i.e. with two joints instead of three, this peculiarity (called "brachydactylism") is sure to be continued in a certain proportion of his descendants; and we call it a "unit-character." The persistence of the Hapsburg lip in the Royal Houses of Austria and Spain is a good instance of how a unit-character comes to stay for many generations. Night-blindness, or the inability to see in dim light, has been traced through a lineage since near the beginning of the seventeenth century—another illustration of the persistence of a unit-character. We do not precisely know what the germinal factors of the unit-characters are like, but in some cases it is known that they lie in linear order in the nuclear rods or chromosomes. In some instances (though it is impossible in a few words to explain *how*) we know what region of the chromosome the factor occupies. But the most important point is that the unit-characters (or their factors) behave as if they were definite entities, like the radicals in chemistry, which can be shuffled about and distributed to the offspring in some degree independently of one another. Thus in the lineage of the "night-blind" it was not every individual that showed the peculiarity, but only a certain proportion in each generation.



COMBS OF FOWLS.

A. Single serrated comb, as in Leghorns and Minorcas.

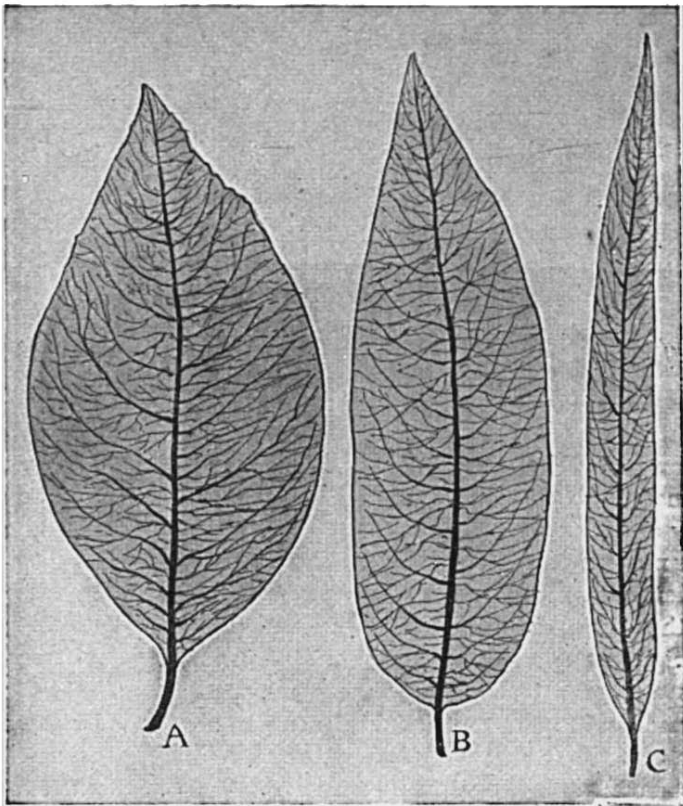
B. Pea comb, with three well-marked ridges of little papillæ, the median one a little higher than the others, as in Indian game-fowls and Brahmas.

C. Rose comb, with a flattened area bearing papillæ, and behind these a pike, as in Hamburgs and Rose-combed Dorkings.

The pea character shows definite dominance, thus pea × single yields pea. The rose character also shows definite dominance, thus rose × single yields rose.

But rose × pea yields out of sixteen cases an average of nine "walnuts," a different kind of comb altogether. The walnut comb has no distinct papillæ like the rose, or ridges like the pea. It shows a corrugated surface suggesting a walnut, and there is generally a curious band of bristles crossing the comb at the beginning of the posterior third. The rest of the members of an average sixteen series from rose × pea are three "rose," three "pea," and one single—a result which admits of reasonable Mendelian interpretation.

In his masterly book on *Mendelism* Professor R. C. Punnett refers to a unit-character as fol-



HEREDITY IN WILLOWS.
(*After Wiesner.*)

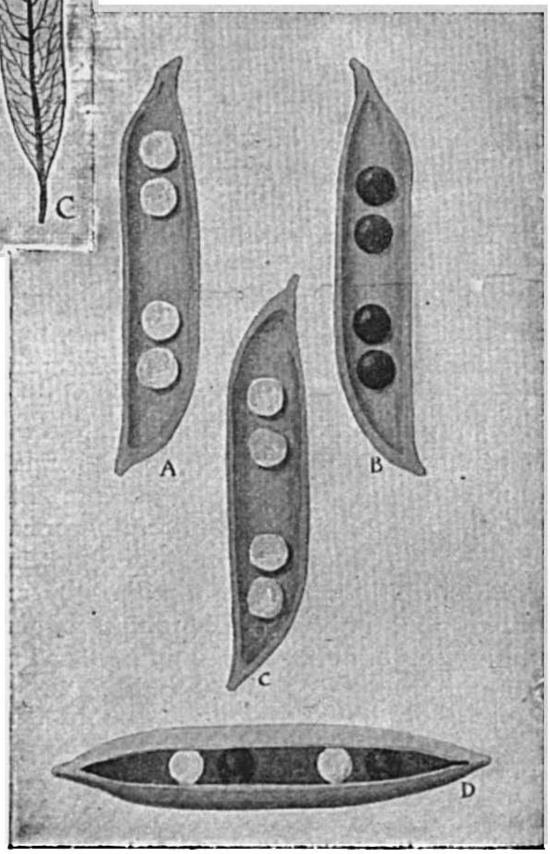
A, a broad-leaved variety, the one parent.
C, a narrow-leaved variety, the other parent.
B, the hybrid offspring, intermediate between the two. This has an appearance of *blending*, but it may be a case of imperfect dominance, as in the Andalusian fowls. Or it may be that the shape of the leaf depends upon a number of Mendelian unit characters which are not linked together but produce an appearance of blending by their fortuitous distribution in the offspring. If some come from the one parent and some from the other they may neutralise one another, with an *apparent* "blend" as the result.

lows: "Unit-characters are represented by definite factors in the gamete [or germ-cell], which, in the process of heredity, behave as indivisible entities, and are distributed according to a definite scheme. The factor for this or that unit-character is either present in the gamete or it is not present. It must be there in its entirety or be completely absent."

§ 6

The *second* fundamental idea in Mendelism is that of *dominance*. When Mendel crossed a pure-bred tall pea with a pure-bred dwarf pea the offspring were all tall. So he called the quality of tallness dominant to the recessive quality of dwarfness, which the hybrid offspring kept, as it were, up their sleeve. The dwarfness is not expressed in the hybrid peas, but it must be part of the inheritance, for it reappears in a quarter of the progeny of the hybrids if these are inbred or allowed to self-fertilise.

The Japanese have reared a race of peculiar waltzing mice, which have many strange habits, *e.g.* of dancing round and round. If a Japanese waltzing mouse is crossed with a normal mouse, all the hybrid offspring are normal, the waltzing peculiarity being recessive to normality. But if these hybrid mice are paired together, some of their progeny



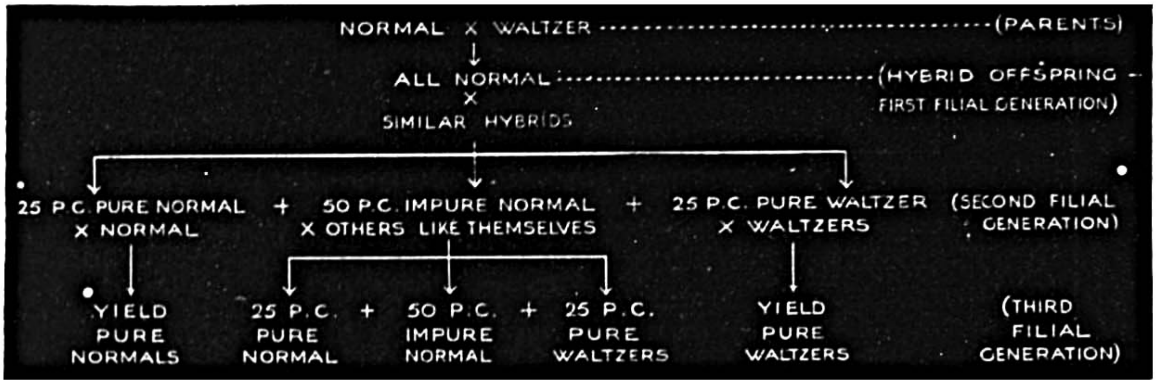
MENDEL'S LAW ILLUSTRATED IN PEAS.

A. Pod of a yellow-seeded pea, the one parent (dominant as to seed-colour).

B. Pod of a green-seeded pea, the other parent (recessive as to seed-colour).

C. Pod of the hybrid offspring (the first filial generation), with only yellow seeds. Yellow-seededness is dominant and green-seededness recessive.

D. The next generation (the second filial generation) shows the occurrence of both yellow seeds (left light) and green seeds (shaded dark).



are waltzers—in the proportion of one waltzer to three normals, which is called the Mendelian ratio. If one of the waltzers of the second generation pairs with another waltzer, the progeny are all waltzers, which shows that the factor for normal locomotion has disappeared from the inheritance along this line. It is a curious fact that one of these second generation waltzers might be conscientiously sold in the market as a pure waltzer, although its parents were normal and one of its grandparents likewise. To return to the beginning, if a waltzing mouse is crossed with a normal mouse, all the offspring will be normal. Normality is dominant; waltzing is recessive. If these normal hybrids pair, their offspring will be 25 per cent. pure waltzers and 75 per cent. apparently normal mice. But of the 75 per cent. apparently normal a third will be pure normals, yielding nothing but normals when bred with others like themselves. But the other two-thirds, though apparently normal, have, like their immediate parents, the waltzing character up their sleeve, for when they are paired together they yield 25 per cent. pure normals, 50 per cent. apparent normals, and 25 per cent. pure waltzers. It is impossible to keep this clearly in mind without some schematic formulation, such as the above.

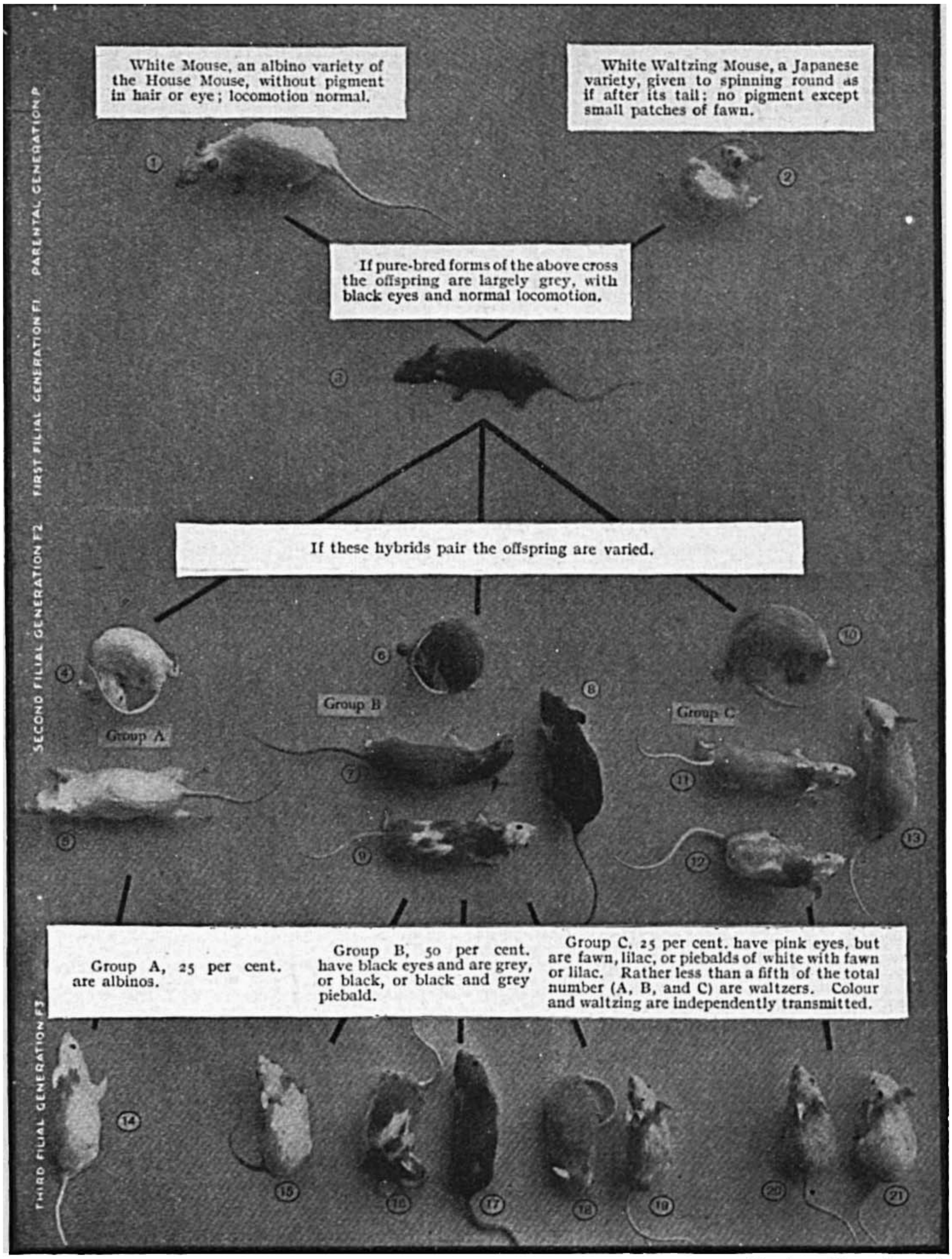
In the case of the mice the character of normal locomotion is dominant over the recessive character of waltzing, but it must not be supposed that the dominant character is necessarily the one nearest the normal type. Thus a short tail in cats is dominant (somewhat imperfectly) to the ordinary tail; the appearance of extra toes in poultry is dominant to the presence of the normal four toes; hornlessness in cattle is dominant to the presence of horns.

Among the many characters which are now known to exhibit Mendelian inheritance, the following may be cited, the dominant condition being named first in each case: Normal hair and long Angora hair in rabbits and guinea-pigs; kinky hair and straight hair in man; crest and no crest in poultry; bandless shell in the wood-snail and banded shell; yellow cotyledons in peas and green ones; round seeds in peas and wrinkled forms; absence of awn in wheat and its presence; susceptibility to "rust" in wheat and immunity to this disease; two-rowed ears of barley and six-rowed ears; markedly toothed margin in nettle leaves and a slightly toothed margin. Why one character should be dominant and another recessive is not known: a positive feature, like a banded shell in the snail, may be recessive; and a negative feature, like hornlessness in cattle, may be dominant.

It should be noted that in many cases of Mendelian inheritance the dominance in the offspring is not complete; thus, if black Andalusian fowls be crossed with white ones the progeny are "blue" Andalusians—a sort of diluted black. These "blue" Andalusians do not breed true; when paired together they yield 50 per cent. "blues," 25 per cent. blacks, and 25 per cent. peculiar whites splashed with grey.

§ 7

The *third* fundamental idea in Mendelism is perhaps more difficult to grasp than the others. Mendel supposed that the hybrid between the tall pea and the dwarf pea produced two kinds of germ-cells in approximately equal numbers—one contingent carrying the factor for tallness and the other contingent carrying the factor for



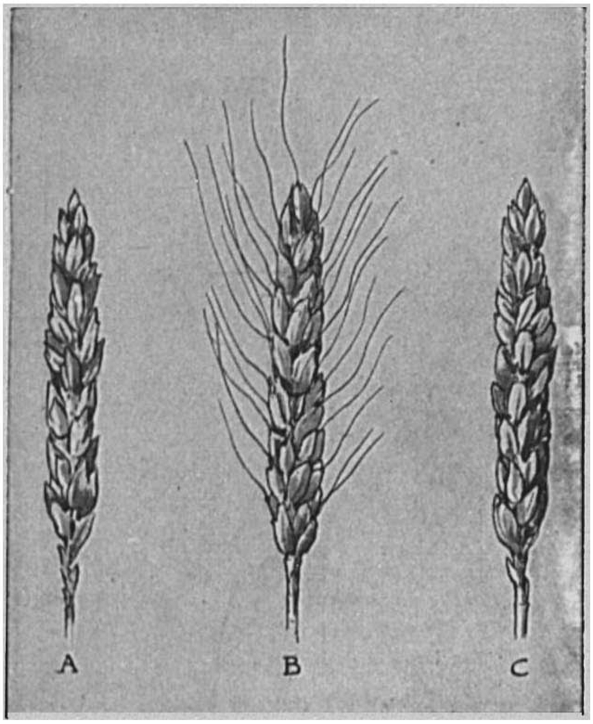
Members of Group A mated together produce only albinos like themselves.

Members of Group B mated together produce greys only like (3), or a mixed litter of albinos, greys, fawns, and piebalds of these.

Members of Group C mated together produce fawns, lilacs, piebalds of these, and an occasional albino.

Photo: British Museum (Natural History).

MENDELISM IN MICE.



MENDELIAN INHERITANCE IN WHEAT.

(*After R. H. Biffen.*)

A. Stand-up wheat, with no beard, the one parent.
B. Bearded wheat, the other parent.
C. The hybrid offspring, with no beard.

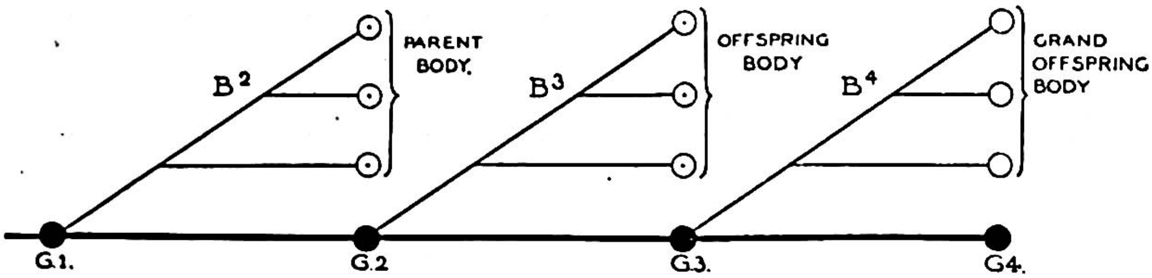
This shows that the beardless condition is dominant and the bearded condition recessive.

dwarfness. In other words, each germ-cell is "pure" with respect to the factor of any particular unit-character. Suppose a long-haired rabbit crossed by a short-haired rabbit, the offspring will be all short-haired. But out of eight ova produced by a female hybrid offspring, four will have the factor for long hair and four the factor for short hair. Similarly, out of eight sperm-cells produced by a male hybrid offspring, four will have the factor for long hair and four the factor for short hair. Suppose these hybrids interbreed, and the fertilisation of the ova by the spermatozoa is fortuitous, then two egg-cells with the short-hair factor will be fertilised by two sperm-cells with the short-hair factor, yielding two quite pure short-haired offspring; two egg-cells with the long-hair factor will be fertilised by two sperm-cells with the long-hair factor, yielding two quite pure long-haired offspring; two egg-cells with the short-hair factor will be fertilised by two sperm-cells with the long-hair factor, yielding two impure short-haired offspring like the hybrid parents; and, finally, two egg-cells with the long-hair factor will be fertilised by two sperm-cells with the short-hair factor, yielding other two impure short-haired offspring like the hybrid parents. So the result must be two pure short-haired offspring, plus four impure short-haired offspring, plus two pure long-haired offspring. If the impure short-haired rabbits are interbred, their offspring (the third filial generation) will show the same ratio, 1 : 2 : 1, more and more exactly the larger the numbers dealt with.

§ 8

Germinal Continuity.

One of the great post-Darwinian advances is the recognition of the fact of germinal continuity—made clear by Galton and Weismann. While most of the material of the fertilised ovum is used to build up the body of the offspring, undergoing in a very puzzling way differentiation into nerve and muscle, blood and bone, a residue is kept



THE IDEA OF GERMINAL CONTINUITY.

G1. A fertilised ovum developing into a lineage of body-cells (B2) and a lineage of germ-cells (the dark thick base-line). G2. Germ-cell which starts the offspring of the next generation, with its body-cells (B3) and its germ-cells along the base-line. G3. A germ-cell starting the grand-offspring, with its body-cells (B4), e.g. ectoderm, mesoderm, and endoderm, and likewise its germ-cells along the basal "germ-track," G3 to G4.

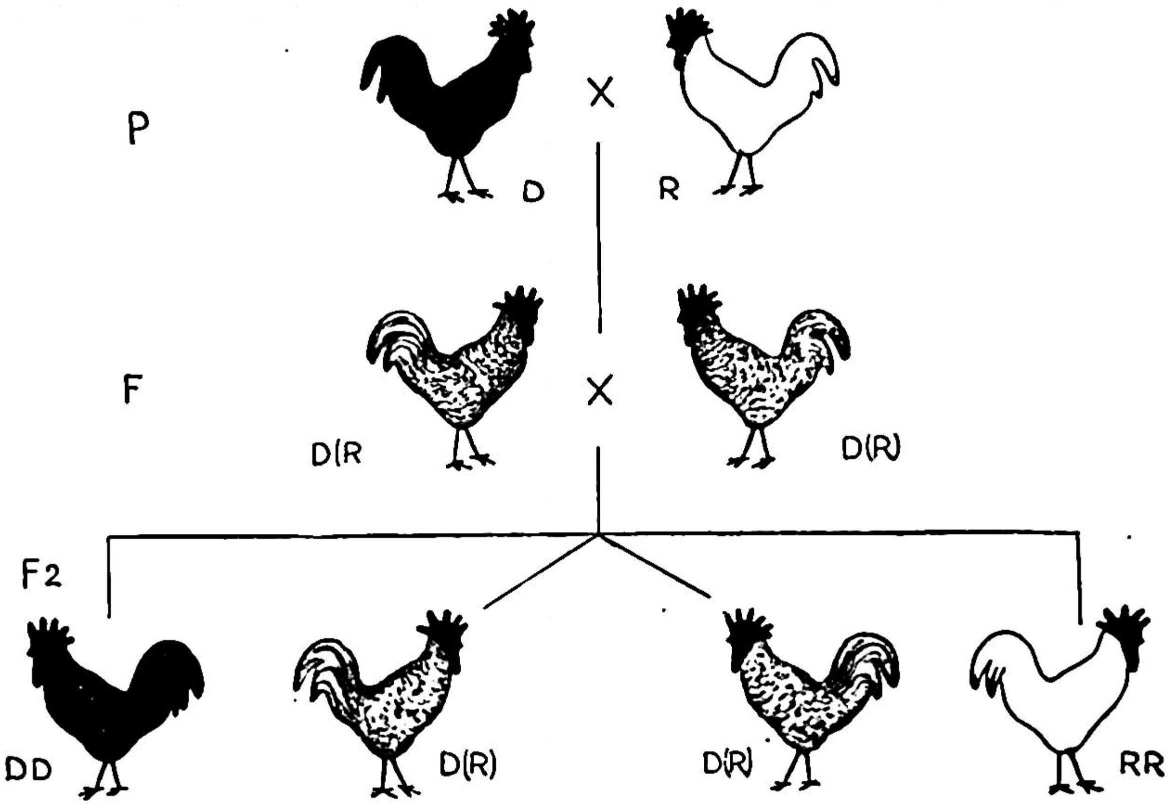
The base-line represents the lineage or chain of germ-cells; B2, B3, B4 are the bodies of three successive generations which fall off from the chain. The fundamental idea is that a fertilised egg-cell gives rise to a body *and* the germ-cells of that body.

intact and unspecialised to form the beginning of the reproductive organs of the offspring, whence will be launched in due course another organism on a similar voyage of life. The reproductive cells of any organism are the outcome of embryonic cells which did not share in the upbuilding of that organism, but continued the germinal tradition unaltered. This is suggested clearly in a diagram slightly modified from one devised by Professor E. B. Wilson. Thus the parent is rather the trustee of the germ-plasm than the producer of the child. In a new sense the child is a chip of the old block. The old question was: Does the hen make the egg, or the egg the hen? The modern answer is that the fertilised egg makes the hen *and the eggs thereof*. The fact of germinal continuity explains the inertia of the main mass of the inheritance, which is carried on with little change from generation to generation. Similar material to start with; similar conditions in which to develop; *therefore* like tends to beget like. As Professor Bergson puts it, "life is like a current passing *from germ to germ* through the medium of a developed organism."

§ 9

As regards Selection.

When we are interpreting the past history of animals, we utilise factors which are seen in operation to-day, just as the geologist does when he is interpreting scenery. It is satisfactory, therefore, that post-Darwinian investigations have *demonstrated* some modern instances of selection *at work*. Let us take a simple case. The Italian naturalist Cesnola tethered some green Mantises with silk thread on green herbage, and found that they escaped the eyes of birds. Similarly, when the brown variety was tethered on withered herbage. But green Mantises on brown herbage and brown Mantises on green herbage



MENDELIAN INHERITANCE IN ANDALUSIAN FOWLS.

(*After Darbishire*)

P, the parents, black (dominant) and white (recessive)
F1, the hybrid generation, "blue" Andalusians, illustrating imperfect dominance.
F2, the second filial generation: 25 per cent. pure blacks ("extracted pure dominants"), DD; 50 per cent. "blues" (impure dominants), D(R); and 25 per cent. whites (extracted recessives), with occasional black spots (RR)

HALF-LOP RABBIT.

A half-lop rabbit, after Darwin, an instance of a variation which seems to be rather uncertain in its inheritance. The peculiarity is that one of the ears hangs down, whereas in "full-lops" both ears do. The pendent ear is often broader and longer than the upright one, an unusual asymmetry. Darwin noted that when the half-lopped condition occurs, whether in one parent only or in both, there is nearly as good a chance of the progeny having both ears full-lop as if both parents had been full-lopped.

were soon picked off. Discriminate selection was at work.

When we are concerned with making a good lawn we may pursue two methods. We may eliminate the weeds or we may foster by suitable tonics the growth of the grass. Similarly, in Nature's sifting there is *lethal selection*, which works by eliminating the relatively less fit to given conditions of life, and there is *reproductive selection*, which works through the predominant increase of the more successful. Darwin never thought simply of Natural Selection; he always emphasised its manifold and subtle modes of operation. He saw, for instance, what some of his successors missed, that the sifting need not in the least involve a sudden cutting off of the relatively less fit, for a shortened life and a less successful family will in the long run bring about the same result as a drastic pruning. It should not be necessary to point out that "the survival of the fittest" does not *necessarily* mean the survival of the strongest or cleverest or best; it simply means "fittest" relatively to particular conditions. The tapeworm is a fit survivor as well as the Golden Eagle.

Darwin realised what some of his successors have missed, that even slight peculiarities may be of critical moment when tested in relation to the complex web of life in which the creature has its being. This is very important in regard to the general progressiveness of evolution—that new departures are sifted in reference to a slowly wrought out and firmly established system of inter-relations. (See the article on Inter-relations.)

§ 10

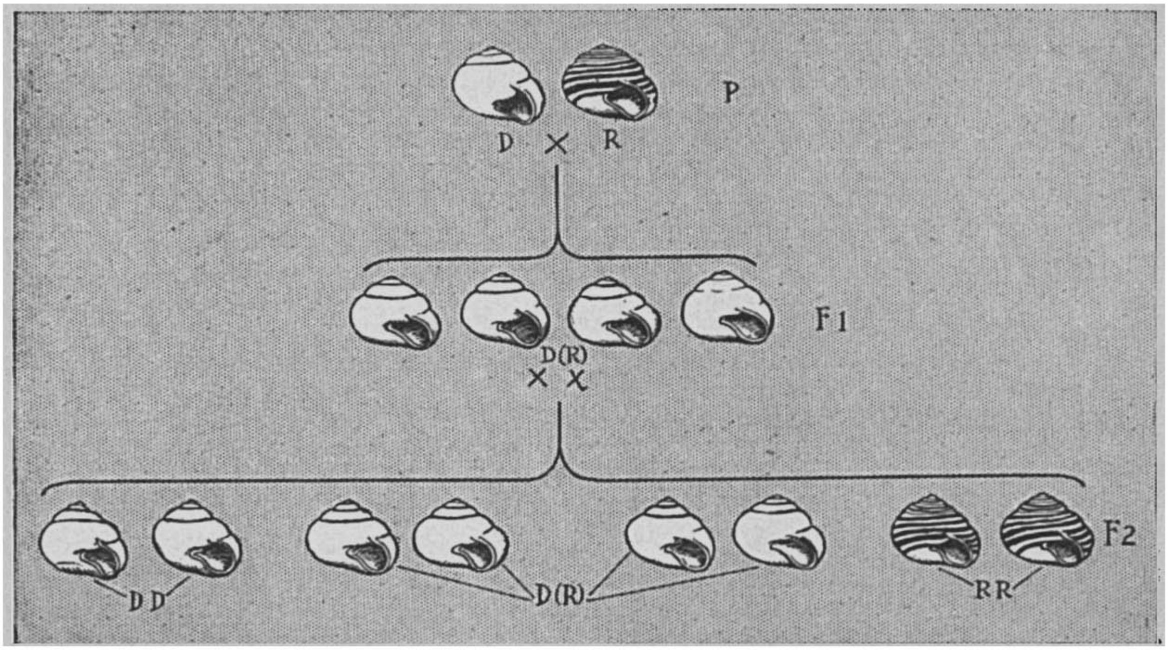
Sexual Selection.

Many male animals, such as stags, antelopes, sea-lions, black-cock, and spiders, fight with one another at the mating time, competing for the possession of females. According to Darwin, "the strongest and, with some species, the best-armed of the males drive away the weaker; and the former would then unite with the more vigorous and better-nourished females, because they are the first to breed. Such vigorous pairs would surely rear a larger number of offspring than the retarded females, which would be compelled to unite with the conquered and less powerful males, supposing the sexes to be numerically equal; and this is all that is wanted to add, in the course of successive generations, to the size, strength, and courage of the males, or to improve their weapons" (*Descent of Man*, 2nd ed., p. 329). Similarly, there would be a premium on those male characters that are useful in the recognition and capture of the females, e.g. large olfactory feelers in moths and strong claspers in skates.

The term "sexual selection" was used by Darwin to include all forms of sifting in connection with mating, but prominent among these was the preferential behaviour of the female. "Just as man can give beauty, according to his standard of taste, to his male poultry . . . so it appears that female birds in a state of nature have, by a long selection of the more attractive males, added to their beauty or other attractive qualities." In the courtship, which is often elaborate, the female selects—in a literal sense.

Darwin was well aware of difficulties besetting his theory of sexual selection, and his fellow-worker Alfred Russel Wallace was one of his severest critics. There has to be proof that some of the males are actually disqualified and left out in the cold. But Darwin indicated that the sifting would work even if the less successful males were not entirely eliminated. Moreover, in some cases the female's preference goes to great lengths; thus a female spider often kills a suitor who does not please her.

It is difficult, again, to prove actual "choice" on the female's part. But there are undoubted cases of preferential mating, whatever the psychology of the process may be. Some critics, like Wallace, have pointed to the difficulty of crediting the female with a capacity for appreciating slight differences in the decorativeness, agility, or musical talent of her suitors. But the modern answer is simply that the accepted mate is the one that most strongly evokes the



INHERITANCE IN SNAILS, WITH BANDLESS AND BANDED VARIETIES.

(*After Lang.*)

When bandless Wood-Snails (*Helix nemoralis*) or bandless Garden Snails (*Helix hortensis*) are crossed with banded individuals of these species, each will make a nest in the ground and deposit half a hundred eggs or more. A snail is always hermaphrodite, producing eggs and sperms; but the eggs of one snail (banded, let us say) are fertilised by the sperms of another snail (bandless, let us say). Let us follow the eggs of a banded individual, fertilised by the sperms of a bandless individual snail. They will develop into individuals whose shells are all bandless, D(R). The negative quality "bandless" (D) is dominant; the positive quality "banded" (R) is recessive. If the bandless hybrids (F1) pair together, the offspring (F2) will be: 25 per cent. pure bandless—extracted dominants (DD); 50 per cent. impure dominants, D(R), in appearance bandless; and 25 per cent. pure banded—extracted recessives (RR). If we had started with the eggs of a bandless individual, fertilised by the sperms of a banded individual, the result would have been the same.

pairing instinct, and that it is not necessary to credit the female with any analytic weighing of the merits of the various males. The details must count, if there is anything in the theory, but they may count, not as such, but as contributing to a general impression of interesting attractiveness.

To point out that certain masculine features, such as antlers, are congruent with the male constitution, just as certain feminine features, such as functional milk-glands, are congruent with the female constitution, is getting behind the question of selection to that of the origin of the variations which form the raw materials of the sifting process—an interesting line of inquiry which has been followed by Geddes and Thomson in their *Evolution of Sex*.

Another important consideration arises when we think of the frequent intricacy and subtlety of the courtship habits (see Pycraft's *Courtship of Animals*). There must be some deep racial justification for this. Groos has suggested that the female's coyness is an important check to the male's passion, which tends to be too violent. Julian Huxley has suggested from his fine study of the Crested Grebe that the courtship ceremonies establish emotional bonds which keep the two birds of a pair together and constant to each other.

§ II

CONCLUSIONS

1. If Darwinism means the general idea of evolution or transformism—that higher forms are descended from lower—then it stands to-day more firmly than ever.

2. If Darwinism means the particular statement of the factors in evolution which is expounded in *The Origin of Species*, *The Descent of Man*, and *The Variation of Animals and Plants under Domestication*, then it must be said that while the main ideas remain valid there has been development all along the line. Darwinism has evolved, as every sound theory should.

3. In regard to the raw materials of evolution, there is greater clearness than in Darwin's time as to the contrast between intrinsic variations of germinal origin and bodily modifications imprinted from without, and there are grave reasons for doubting whether the latter do as such affect the race at all. There is still to be heard the slogan "Back to Lamarck!" but there can be no return to any crude Lamarckism. If the individual gains and losses, the individual indents and prunings, really count as such in racial evolution, it must be in some subtler way than is suggested by the giraffe getting its long neck by ages of stretching, or the deep-sea fish becoming blind by generations of darkness and disuse. There should be no haste to close any door of reasonable interpretation, still less of experimental inquiry, but there is at present amongst zoologists widespread agreement with Sir Ray Lankester's pronouncement that one of the notable advances since Darwin's day has been getting rid of the Lamarckian theory of the transmission of individually acquired characters or imprinted bodily modifications. Of course, counting of heads is no argument; but the facts are not at present in favour of the Lamarckian view. But we may perhaps look for an evolution of Lamarckism as well as of Darwinism!

4. Darwin based his theory of evolution very deliberately on the fluctuating variations which are always occurring. Given time enough and a consistent sieve (the struggle for existence), will not Nature achieve more or less automatically what man reaches purposefully in his breeding of cattle and cultivating of wheat? But modern Darwinism, while holding fast to this, welcomes the demonstration that brusque discontinuous variations or mutations are common, and that they are very heritable. All of a sudden, it appears, the sporting Evening Primrose may produce an offspring which is potentially a new species.

5. Darwin meant by "fortuitous variations" that he could not give any formula for the causes of the novelties he observed. No doubt he also meant that the organism in varying was not aiming at anything. And yet he laid great stress on what he called "the principle of correlated variability"—an idea of great importance—that when one part varies other parts vary with it, "being members one of another" as St. Paul said. In other words, a particular germinal change may have a number of different outcrops or expressions. But the more correlation there is, the less reasonable will it be to speak of fortuitousness. And one of the changes since Darwin's day is the recognition that variations

THE RUFF (*MACHETES PUGNAX*).

(*From specimens.*)

The Ruff is a polygamous bird of the plover family. It used to nest abundantly in Britain, but is now hardly more than a bird of passage. In winter the two sexes—ruffs and reeves—are very similar in plumage, but the females are smaller. At the breeding season in spring there is very marked sex-dimorphism. The face of the male becomes covered with little yellow warts, the head is adorned with erectile tufts of feathers, and the fore-neck develops a large "ruff" of feathers which can be raised and depressed according to the state of excitement. In the tufts and the "ruff" there is extraordinary variability of colouring, e.g. white, rufous, or black, with or without bars. It is said that no two are alike. This illustrates the occurrence of countless small variations. The males assemble in little parties at the breeding-time and fight with great vigour hour after hour, but without doing much damage. According to Darwin's theory of sexual selection the tournaments have been factors in the evolution of the sex-dimorphism.

are often very definite—just as they are among crystals.

6. Another change from Darwin is the Mendelian idea of unit-characters, which behave like entities in inheritance. They are handed on with a strong measure of intactness to a certain proportion of the offspring. Their "factors" in the germ-cells are either there or not there. Sometimes, at least, these unit-characters arise as mutations, and thus we have an answer to Darwin's difficulty that abrupt changes would be averaged off in intercrossing. Unit-characters do not blend.

7. Since Darwin's day there has been, in a few cases, definite proof of natural selection at work; the different forms of selection have been more clearly disentangled; the subtlety of Darwin's idea of selection has been confirmed; the reality and the efficacy of preferential mating has been much criticised, but Darwin's theory of sexual selection has in its essentials weathered the storm. In proportion as new departures come about suddenly by brusque mutation, the burden to be laid on the shoulders of selection will be lessened. In so far as the selection is in relation to a previously established system of inter-relations, there will be a reduction of the fortuitous in the process; and the same will be true in proportion to the degree in which the organism takes an active share in its own evolution—as it often does.

8. Modern biologists are inclined to put more emphasis on "Isolation" than Darwin did, meaning by "Isolation" all the ways in which the range of intercrossing is restricted and close in-breeding brought about.

When we use the term Darwinism to mean, not his very words, but the living doctrine legitimately developed from his central ideas of variation, selection, and heredity, we may say that Darwinism stands to-day more firmly than ever. It has changed and is changing, but it is not crumbling away. It is evolving progressively.

This is only an "outline" of a great subject, and it is not an article that he who runs can read. It is very important to avoid dogmatism in regard to an inquiry which is still relatively young. There was not much scientific evolutionism before Darwin's day. The writer has not concealed his opinion in regard to such a question as the transmission of acquired characters, but it is not suggested that this is the only possible opinion. It may be recommended that readers to whom the subject is comparatively new, and to whom it appears full of uncertainties, should write out their ideas in a definite way and then compare them carefully with the relevant paragraphs in the article. It is all too easy to go off on a wrong tack, and this should be guarded against by patient study. For the problems of evolution are fundamental.

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