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EVOLUTION

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EVOLUTION

BY

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PREFACE

This book owes its origin to the fact that no existing general treatise on evolution develops anything like what the author regards as the present-day concept of that process. Books there are, enough of them and perhaps to spare. In them the paleontological evidences of evolution are described, adaptations are classified and more than sufficiently illustrated, the bearing of homology of various animal features on kinship is described in classical fashion, lines of evolution are abundantly traced, and many other things related which are calculated to convince the most skeptical person that evolution really has happened. Added to these discussions are sometimes emotional appeals to the love of truth and for the security of free thinking, attempts to smooth over the rugged zone between science and tradition, pleasant or unpleasant predictions of man's future, efforts to relate evolution to change in the social order, and sometimes a bit of metaphysics. There are, it is true, valuable articles and occasional books on limited portions of the evolution problem; the statements above apply to those which aim, or which because of their obviously intended audiences should aim, to be general.

Unfortunately for the use of extant treatises, the group for which the present book is intended, a class of college students, does not require many of the things mentioned. With rare exceptions they do not need to be convinced of the fact of evolution. The tribulations of science versus tradition do not greatly concern them. And as for the predictions of man's future advance or decline, they are no more egocentric than are other people who live chiefly in the present. What they should know of the whole business of change of species is largely the how and why. On this subject the general books on evolution have been either reticent or—may it be said?—outmoded. Particularly have they lacked any adequate application of knowledge of genetics to the problems of evolution. Every such book has recognized that evolution rests on heredity, and has included an account of the simpler facts of Mendelism. But not one of them

that is at all general in scope attempts to show precisely how evolution must work in the presence of the typical heredity mechanism. Fortunately for genetic explanations one may now go much farther than would have been possible only a few years ago. The splendid work of Wright, Haldane, and Fisher in tracing the results of chance, and of some of the special features of the operations of heredity, has laid open an extensive field that had seemingly been closed.

Under these several circumstances it is desirable that some one should attempt to review the field of evolution as it appears to modern biologists, with the genetic bearings indicated wherever these may reasonably be assumed. The author's interest in evolution is almost solely in its initiating causes and guiding agencies. Since, however, even those who are reasonably certain that evolution has taken place should be able to defend that conclusion if necessary, the usual classes of evidence have been reviewed. That is done briefly in the first four chapters. The rest of the volume is devoted to agencies, with sporadic incursions into the history of the idea and of evolution itself. How well the process has been conceived the geneticists will no doubt be best able to judge.

A. FRANKLIN SHULL.

ANN ARBOR, MICHIGAN,
March, 1936.

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EVOLUTION

CHAPTER I

ORDER IN DIVERSITY AMONG LIVING THINGS

> That it is possible to arrange all the varied forms of animals into groups, having this sort of singular subordination one to the other, is a very remarkable circumstance. T. H. HUXLEY, 1863.

The living things on the earth present an almost inexhaustible array of differences. Professional naturalists give testimony to the variety of life by becoming what are called ornithologists, mammalogists, conchologists and the like, thereby confessing their inability to master more than a small section of the living world about them. How great this diversity is can be expressed numerically, but to do so it is necessary to decide upon the degree of analysis to which populations shall be subjected. If every detectable difference be recognized, it is probably true that no two organisms are alike; with such a standard the number of different kinds of beings is the number of individuals, which is almost inexpressibly large. If minor differences are to be ignored, then individuals must be grouped, and the number of groups depends on how large are the neglected distinctions. This is what taxonomists do in classifying both plants and animals—the greater the differences which they pass over, the fewer the resulting groups. In general classifications have sought to recognize all significant heterogeneity up to the point at which the number of groups becomes unwieldy. Taxonomists have disagreed concerning what is significant, and have differed in their opinions of what constitutes a too cumbersome system. At the present time, among animals, about 800,000 kinds have been described; and it is probable that, with the same standards but with all existent kinds discovered, the number would be far over a million. Among plants about 250,000 kinds have been described, and the total including those still unknown is estimated to be perhaps one-fourth larger.

Degrees of Likeness and Difference.—Naturalists at first supposed that these kinds of organisms, to which they gave the name species, had always existed as distinct from one another as they are now, and in the same form as at present. How these species were believed by early naturalists to have sprung into existence is immaterial to the present discussion. It must suffice to say that whatever that origin was thought to be, it was regarded as being independent of the origins of other species. There are, however, within the classifications themselves, indications that such independence did not exist. When species are compared with one another, it is found that they display very unequal likenesses and differences. It is not possible to arrange them in a series from one extreme to another with evenly graded steps between the species. Even when a very limited portion of the animal or plant kingdom is employed for this purpose, such arrangement with uniform steps is still impossible. This is not due merely to the fact that species differ in several or many characters, and that an evenly graded series based on one character cannot be dovetailed into a series based on some other character. It is due rather to the fact that some species resemble each other much more closely than they resemble any other species. Half a dozen or more species of animal differ from each other in relatively small ways; but when the rest of the animal kingdom is searched for others as nearly like them, none is found. The most similar other species is separated from them by a more distinct gap. This most similar other species may be one of another half dozen or more which exhibit among themselves as great a degree of similarity as did the first half dozen, but this group is separated from the first by a greater difference than that between any two species within either of the groups. All through the animal and plant kingdoms species are capable of being thus grouped. The number of species in any such group varies greatly; occasionally a species has to be set aside by itself, but often there are scores of them in a group. This clustering of species is not merely something which the taxonomist may do if he chooses; it is something he must do if his arrangement follows the observed properties of the species.

Now, the different degrees of similarity and difference among species which make their collection into groups the obvious way of arranging them are hardly consonant with the view that

the various species are and always have been independent of one another. If species were from the beginning independent, there would be no obvious reason for the existence of groups based on similarity. When the first few drops of a shower fall upon a dry pavement, they are not disposed in clusters according to

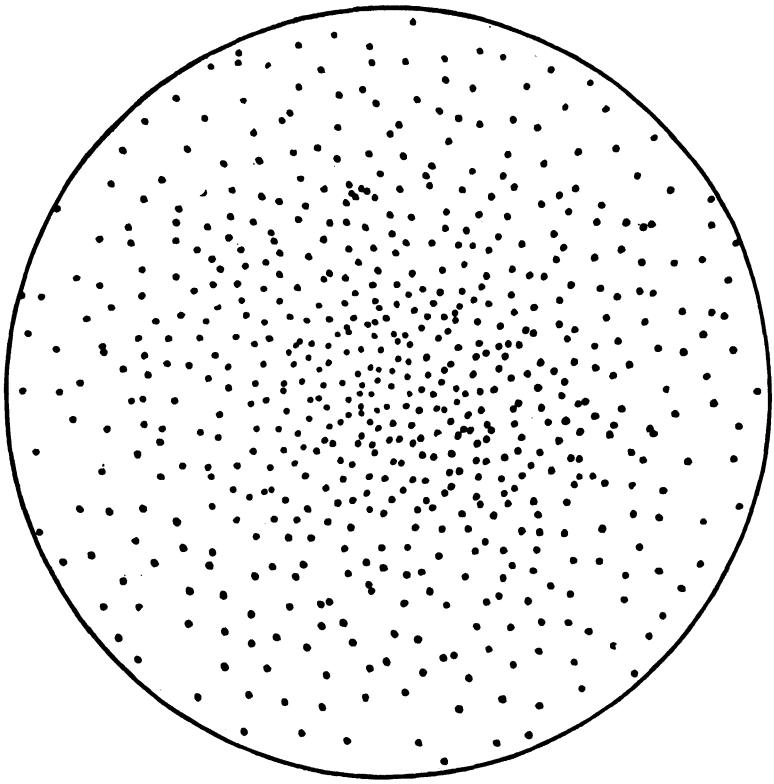


FIG. 1.—Distribution of shot on a target. (*Courtesy of Remington Arms Company.*)

any scheme. The shot from a shell when fired at a target (Fig. 1) are not systematically collected into groups separated by spaces of regularly variable widths. It would be difficult to find groups of half a dozen or a score of shot, or of rain drops, regularly separated from adjoining similar groups by spaces wider than those between members of the same group. If the shot on a target were distributed in such groups, with wider spaces between clusters than within them (Fig. 2), it would be

inferred either that a number of the lead pellets had clung together for some time after leaving the cartridge but had separated before reaching the target, or that the balls had broken into fragments at some point between gun and target. In like manner, when species are found to be everywhere capable of

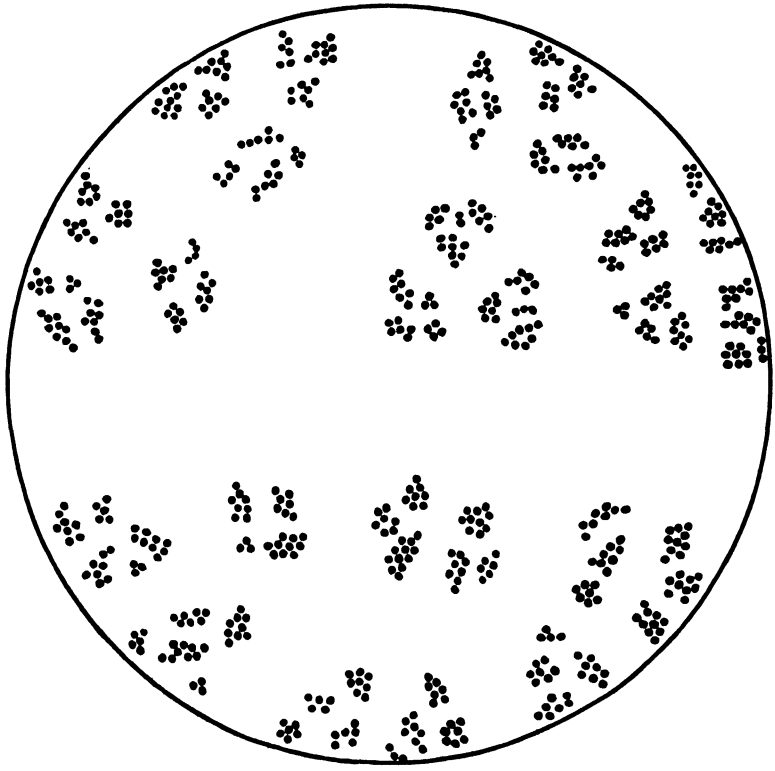


FIG. 2.—A hypothetical grouping of shot on a target which would indicate some connection between the separate pellets—comparable to the grouping of species in genera, families, orders and classes.

being bunched on the ground of similarity, it is difficult to avoid the conclusion that they were, in their origin, in some way associated with one another.

Genera and Higher Groups.—The species that resemble one another closely constitute, in the language of the taxonomist, a genus. It may be useful to illustrate the grouping described above by examples chosen from animals so well known that anatomical bases for the classification will not be required.

These examples are taken from the birds of North America. There are some nine species of gulls belonging to the genus Larus. Likewise, there are in the same region nine species of terns assigned to the genus Sterna. Gulls are not very different from terns, but the difference between them is greater than that between two of the gulls mentioned, or between two of the terns. There are eight species of ducks, one of them the mallard, belonging to the genus Anas, and five geese belonging to the genus Branta. The difference between any one of these ducks and any one of the geese is greater than that between any two of the ducks or between any two of the geese.

The grouping of living things does not stop with the species. The genera are likewise subject to such arrangement. The gulls and terns, including half a dozen genera besides Larus and Sterna, are much more nearly alike than they are like any other birds. The ducks, geese and swans, including a dozen and a half genera besides Anas and Branta, are more alike among themselves than they are like any others. In classification, these closer similarities are recognized by placing the similar genera into a family. The gulls and terns make the family Laridae, while the ducks, geese and swans compose the family Anatidae.

In a similar way families are collected into orders. The gulls and terns (family Laridae), together with two other families (the skimmers, and the skuas and jaegers), constitute one order. The family of ducks, geese and swans constitute an order by themselves, since there is no other family nearly enough like them to be included with them. Other orders of birds are the herons, storks and ibises; the sandpipers, phalaropes and plovers; the grouse, bobwhites and pheasants; the hawks, eagles, owls and vultures; the woodpeckers; the whippoorwills, nighthawks, swifts and humming birds; and the perching birds, such as sparrows, tanagers, swallows, vireos, warblers, wrens and thrushes. To any one familiar with these birds, it is obvious that those included in one order have more in common than any of them have in common with birds of another order.

In the animal kingdom as a whole orders are collected into groups of higher rank known as classes. All the birds belong to one class. Contrasted with them, but more nearly like them than are any other animals, are four other commonly known classes, namely, the fishes, amphibia, reptiles and mammals. Any

bird is more like any other bird than it is like any fish or reptile. Any fish is more like any other fish than it is like any amphibian or mammal.

And yet all these groups (fishes, amphibia, reptiles, birds, mammals) have important things in common, in which they differ from all other animals. Chief among these is the bony skeleton which, in every one of them, includes a segmented axis, the backbone. Another feature is the position of the nervous system above or behind the digestive tract, a position which it occupies in no other group of animals. This greater similarity among these so-called higher animals than between them and any others is recognized in classification by placing them, together with several groups of less commonly known animals, in the phylum Chordata.

There are a dozen other phyla. Without using their technical names, the chief of these phyla may be indicated as follows: the insects, lobsters, centipedes, spiders; the clams, oysters, snails, cuttlefishes; the segmented worms and leeches; the starfishes, sea urchins, sea cucumbers; the roundworms; the flatworms; the hydroids, corals, anemones, jellyfishes; the sponges; and the unicellular organisms or protozoa. While zoologists have attempted at times to discover significant similarities between two phyla, as between insects, centipedes, etc., on the one hand, and the segmented worms on the other, largely because of the segmentation of the bodies in both, or have set one phylum apart as distinct from the rest because of one striking feature, attempts to arrange all the phyla into a small number of comparable groups of still higher rank have been of doubtful validity. That is, the phylum is the most inclusive group all members of which possess undoubtedly significant similarities.[1]

Each phylum is constituted in essentially the same way as is the group Chordata. The Arthropoda, for example, fall naturally into four groups, the crustacea (lobsters, etc.), the centipedes and millipedes, the insects, and the spiders and similar animals.[2]

[1] This statement ignores the fact that, regarding several phyla as proposed by various taxonomists, but not regarding any of the principal ones mentioned in the text, there is difference of opinion as to whether the similarities exhibited are significant. In these exceptional cases there is disagreement concerning the true constitution of the phyla.

[2] There is a fifth uncommon group including only a number of species of the caterpillarlike Peripatus.

Each of these groups, which are called classes, is naturally divisible into smaller groups, the orders. Thus the insects include nineteen (more or fewer, according to different taxonomists) orders, of which the following will serve as illustrations: the bees, ants and wasps; the butterflies and moths; the beetles; the flies; the grasshoppers and crickets; the termites; the dragonflies; and the May flies. Each order is divisible into families, naturally distinguished from one another, each family into genera, and each genus into species. In other words, the whole animal kingdom is classifiable according to the same general scheme. Plants are classified in a strictly comparable way, the only difference being that botanists have applied different names to the groups of high rank.

The Branching Arrangement.—The important feature of the classification is that, according to it, the living world is composed of groups within groups. Regardless of the rank of a group, whether low (species) or high (class), it has certain resemblances which place it nearer to certain other groups of its own rank than to others. Everywhere the genera within one family are more alike than are any of the genera of different families; the families comprising an order are more alike than are any families of different orders; the orders belonging to one class resemble one another more closely than do any two orders of different classes; and so on.

As was pointed out in connection with species, this grouping within groups would not be expected if each group had arisen independently of other groups of the same rank. The several genera of a family must have been in some way interdependent in order that their present-day closer similarities might exist. Those orders which are especially similar, and are marked off from all other orders by greater differences, must have, or must have had, some fundamental connection. The very obvious order which exists amid all the diversity of living things can scarcely be reconciled with a totally independent origin of each of the groups.

It was partly to explain this natural order that the doctrine of origin by evolution was enunciated. This doctrine made use, for all of the groups in the classification, of a principle adopted by everyone as applicable to the members of a species. It has always been recognized, even by those who did not accept the

idea of evolution, that the individuals belonging to one species have sprung from a common ancestry, and that they owe their similarities to inheritance of the ancestral qualities. The principle of descent was used in the oldest taxonomies when males and females very different in form were included in the same species; or when queens, workers and drones among bees, or winged, wingless and gamic aphids were considered single units in classification. If the same reasoning be applied to groups of higher rank, it should be concluded that the species belonging to a single genus have likewise come from common ancestors. In like manner, the genera that are nearly enough alike to be included in one family must, if the principle of similarity due to common inheritance be applied, be supposed to be descended from ancestors common to them but different from the ancestors from which the genera belonging to other families were derived. So also the families of each order must belong to a different line of descent from all families belonging to any other order. All orders comprising one class must have had different ancestors from all orders constituting any other class. And so on to the classes of each phylum.

These assumptions regarding common ancestry are made because no phenomenon of life other than heredity is known which would account for the observed similarities among groups. They entail evolution as a corollary, however, because there are also differences among the similar groups. If several species have sprung from the same ancestors, their differences must have originated somehow in contravention, or as an alteration, of heredity. If numerous genera are descended from the same source to make a present-day family, inheritance must somewhere have been modified to bring about the differences between the genera. If it be assumed that descent may here and there involve modification, it would be expected that living things today would be capable of a branching arrangement, with branches divided and subdivided, that is, they would fall into groups within groups. The branching nature of the classification of animals and plants was observed before evolution was conceived. It was one of the incentives to the adoption of the evolution theory, and is one of the potent reasons for recognizing the truth of that theory.

To avoid confusion it should be pointed out that, in assuming different ancestries for different groups, the time at which the ancestors in question lived is an important consideration. If all vertebrate animals (part of the phylum Chordata) have descended from common ancestors, then two genera of mice have these ancestors in common; also the reptiles and the birds have both descended from these ancestors. The common ancestors of all these vertebrates, however, must have lived a very long time ago. When it is said that the reptiles had different ancestors from the birds, reference is made to the most recent common ancestors of the reptiles and the most recent common ancestors of the birds. These must have been different animals, and must have lived at a time not quite so remote as did the common ancestors of the whole phylum. Likewise, when it is assumed that field mice (several species) had different ancestors from the jumping mice (also several species), it is the most recent common ancestors of the two groups to which reference is made. With this qualification, nearly always implied but seldom expressed, that it is the most recent common ancestors which are meant when common ancestors are mentioned, two or more somewhat similar groups are assumed, on the evolution doctrine, to have had common ancestors that were different from those of certain other somewhat similar groups of the same rank. In general, present-day species must have had relatively recent common ancestors, genera common ancestors not quite so recent, families ancestors more remote, and so on.

Age of Groups of Different Ranks.—From the above considerations it is obvious that on the average species at the present time are younger than genera, genera younger than families, orders younger than classes. It is probably not true that all present species are younger than all genera. A rapid succession of changes in one line of descent might well lead to the amount of differentiation appropriate to half a dozen genera, each divided into several species, and all belonging to one family, while in the same period of time in another line of descent relatively few changes would have given rise only to three or four species. In such a case some of the genera of the former line might be younger than some of the species of the latter. There may well be many cases of such unequal rates of change. Nevertheless, it could

hardly be otherwise than that on the whole species are younger than genera, genera younger than families.

While these statements are probably true regarding species, genera, families, etc., as concrete assemblages of living things at the present time, they should not be true of species, genera and families in the abstract. Species as a category, without reference to any particular species, must be the oldest of all the taxonomic groups, phyla the youngest. For, if life originated but once, and the descendants of the primeval organism inherited all the qualities of their first ancestor without change, there was at that time only one species. When a change occurred, and was transmitted to a group of individuals, two species were then in existence. It was not until one or more of these species became further differentiated into species, and, in their change, had diverged somewhat from the other groups of species being formed at the same time, that anything like a modern genus would arise. With further differentiation, a genus could become a family, each of the former species of the genus becoming, perhaps though not necessarily, a genus of the family. Differentiation must have proceeded far before groups complex enough to compare with present orders or classes would be produced. Phyla would be the last to be formed, and hence, as a category, the youngest.

If the above suppositions are correct, evolution of all the groups has been brought about by the origin or modification of species. A genus is evolved by the splitting of a species into a group of species. A family arises by the breaking up of some or all of the species of a genus into new species. An order is produced when some or all of the species composing a family differentiate into groups of species; for this differentiation should entail a divergence of the species belonging to different genera so as to produce groups of the rank of families. So in the larger groups, it is everywhere by the origin of species out of other species, or by the modification of whole species without breaking up if that be possible, that groups of low rank are converted into groups of high rank—orders into classes, classes into phyla. Evolution in general is thus the origin of species.

Nature of Species.—What, then, is this assemblage called the species? Classification has been discussed in this chapter as if it were a very simple matter. It is, on the contrary, very difficult. Every biologist has a very general idea of what he

means by orders, families, genera and species. Those who engage directly in taxonomic work doubtless have a more definite idea of the content of the various groups than do biologists in general. Unfortunately, however, taxonomists very often disagree. They are often of different opinions whether a genus consisting of two groups of species separated by a slightly wider gap should be two genera or one. In a species not all individuals are alike. Their differences may be hereditary ones, and the differentiating hereditary characters may be possessed by considerable numbers of individuals. Should these types be recognized as two different species? There is no accepted answer to this question. Some biologists make two species of them, others call them varieties of the same species—variety being a rank lower than the species, not mentioned in the foregoing account of classification because it is not always used, that is, not all species are divided into varieties. Other uncertainties in taxonomy concern the allocation of a given species to this or to that genus, when it is almost equally similar to the species of both genera. The same difficulty arises in the allocation of genera to families, and sometimes in the arrangement of even higher groups. That these difficulties are real and frequent is shown by the number of times classifications have been changed, in each of the respects indicated, by different taxonomists.

Only an approximate and somewhat generalized idea of a species can therefore be given. It is a group of individuals most of which possess most of their qualities in common. It differs from all other groups of individuals in one or more respects, usually readily recognizable. Intergrading forms between two species are not common, relatively speaking, so that the separation of species is for the most part rather sharp. There is a strong tendency for different species to occupy different regions. While there may be overlapping of ranges, it is rare that two ranges coincide at all boundaries. It is particularly worthy of note that species differing only slightly are prone to be geographically almost entirely separate, though usually adjoining. There is usually some degree of sterility between species. While some species cross freely and produce fertile hybrids, it is much more common either that two individuals of different species are incapable of producing offspring, or, if they produce offspring, that these offspring are partially or wholly sterile. Species

show a high degree of permanence; that is, over a long period of time members of a line of descent possess largely the same characters. Nevertheless, there is much evidence to show that species possess plasticity; that is, they are subject to a certain amount of change in the course of many generations.

These are the characters of species—similarity of their individuals, difference from other species, infrequency of intergrading forms, a tendency to occupy different regions, the frequency of interspecific sterility, a considerable degree of permanence, and a certain amount of plasticity. It will be necessary to refer to all of them in the discussion of evolution in later chapters.

Adaptiveness of Taxonomic Distinctions.—To many naturalists the fitness of living things to the situations in which they live has seemed the most remarkable thing about them. To all of them, probably, adaptation has appeared to be greater than could be accounted for by mere chance. Doubtless an exaggerated notion of the fitness of animals and plants exists and has long existed; many special features regarded by some naturalists as adaptive probably have no use at all, and other features which are of use are not at all essential to the well-being of their possessors. Nevertheless, after making allowance for mistaken inferences, the nice adjustment of the structural and physiological properties of organisms to the environment is truly remarkable.

This adaptation is very unequally distributed through the several taxonomic ranks. In general it is considerable in the high ranks, slight or wanting in the low ranks. The class of fishes is plainly adapted, by the possession of fins and gills, and by their characteristic body form, to an aquatic habitat. Birds (with some exceptions) are as obviously adapted to aerial locomotion. In none of the other classes of vertebrate animals does any such distinctive adaptation extend throughout the group, and in almost none of the classes of invertebrate phyla is the adaptive relation so simple and extensive. Among orders, to consider only mammals because they are popularly well known, the group of bats is strikingly adapted to flight, and the seals and walruses, also the whales, and the sea cows, to aquatic life. These are conspicuous adaptations because other mammals are confined to the surface of the land or to trees.

The rodents (an order) lack canine teeth, but have continuously growing incisor teeth, which they use for gnawing. The marsupial mammals (an order) possess ventral pouches, an adaptation to protection of the young, which are exceptionally immature at birth. Among families, the moles are adapted to burrowing, the opossums to life in the trees, the beavers to a semiaquatic existence, while the porcupines are exceptionally protected by their quills against enemies. It should be understood that not all differences between groups of these higher ranks are so adaptive as these; the ones named are outstanding examples of usefulness. There are some class, ordinal and family distinctions which are not obviously and markedly useful to their possessors. The probable reason for the existence of both adaptive and nonadaptive taxonomic differences will appear in a later chapter.

When one descends to genera, it is much more difficult to point out the adaptive significance of the distinguishing features. The panthers and jaguars constitute one genus (Felis), and the lynxes and bobcats another genus (Lynx), the only North American genera of the cat family. One of the differences between them is that the former group have one more upper premolar tooth on each side than the latter. It is almost inconceivable that this difference is of any functional significance in the lives of these animals. There are other differences between the two genera, size being one of them. The panthers and jaguars are larger than the lynxes and bobcats, and advantage is taken of their larger size by the former to pursue larger game (deer and sheep, as compared with rabbits and smaller mammals taken by the lynxes). But the adaptive significance of size is small compared with that of the family characters possessed by both of these genera—their lithe muscular bodies, sharp, retractile claws, and the shearing (noncrushing) form of their teeth in general. Obviously adaptive generic characters are those of the muskrats (genus Ondatra), particularly their broad feet, the hind ones partially webbed, their dense waterproof underfur, and their laterally compressed tails. With these characters, it is not surprising to find muskrats always near water, and preferring swimming to locomotion on land.

In the difference between two species of the same genus it is usually impossible to see any adaptation. In the mammals, such differences often involve chiefly color or size, and are slight.

Two species of chipmunk differ by less than 10 per cent in size, and the outer stripes of one are less conspicuous than those of the other. Two species of white-footed mice differ mostly in shades of color; their size is nearly the same. Of two porcupine species, one has hairs tipped with yellowish white, the other tipped with greenish yellow, and the latter is a little smaller. One hare has grayish to buffy brown pelage, its feet gray on top; another hare is reddish brown with more reddish feet, and is an inch shorter. These examples will suffice. In all the animal kingdom, such differences between species can be duplicated with respect to their functional insignificance. Indeed, it is hard not to duplicate them. It is exceptional to find that the difference between two species of the same genus is advantageous to either species. Naturalists have sometimes pointed out that man's inability to see the usefulness of these distinctions may only be a result of his dullness of perception and understanding. This comment is usually designed to remove a stumbling block in the way of a particular theory of evolution. As an argument it is two-edged, however. If we are to decline to recognize lack of adaptation because of our ignorance, we should be as ready to acknowledge that some things that look adaptive to us really are not so. This latter attitude would doubtless have saved more false steps in evolution theory than the former. It is a more logical procedure to accept the evidence as it appears, and attempt to discover what it means, rather than argue it away.

Taking the evidence regarding the adaptiveness of taxonomic distinctions at its apparent value, one must conclude that the characters of the higher ranks (classes, orders, families) are often, perhaps usually, adaptive, those of genera less often or less certainly so, while specific distinctions are usually not adaptive. If the origin of the various groups is what the classification itself suggests it to be, species arising first and gradually evolving into the higher and higher groups, it means that adaptation lags behind evolution. This has an important bearing upon at least two evolution theories to be discussed later.

CHAPTER II

THE SIMILARITIES INDICATING KINSHIP

> There can be but one perfect method of [classification], which is the natural method . . . each being is determined by its resemblance to others, and difference from them. BARON CUVIER, 1828.

The likenesses in accordance with which animals and plants are grouped in a classification have been alluded to in the preceding chapter mostly in very general terms. The taxonomic groups were illustrated with animals so well known and so obviously similar within the groups but different as between groups, that descriptions of the similarities and differences were unnecessary. It was only in connection with possible adaptations that concrete examples of distinguishing characters were mentioned. To convey to nonbiological readers an adequate notion of the grounds for attributing such resemblances to heredity and hence to descent from common ancestors, it seems desirable to enumerate or describe some examples. The study of zoology and botany, especially the branch of comparative morphology (or anatomy), is replete with them. Indeed, in so far as these sciences deal with classification, the characters possessed in common constitute their entire subject matter. Reference can be made here to only a few such characters.

Taxonomic Characters.—The characters most obviously useful for delimiting taxonomic groups are those possessed by only one group, lacking in all others of the same rank. Among the phyla, the group to which the jellyfishes, hydroids and sea anemones belong (coelenterates) is thus distinguished by stinging cells (Fig. 3); every coelenterate possesses these organs of attack and defense, and no other phylum has them. The phylum of sponges has, within the passages through which water circulates, layers of cells each having a flagellum surrounded by a collar (Fig. 3); no other phylum of multicellular animals has such collared cells, though certain of the single-celled organisms have collars. Only one phylum has a horny skeleton on the outside

of the body; that group (arthropods) includes the insects, crustacea, spiders, centipedes, etc. The only phylum possessing an internal skeleton of bone is that of the chordates (fishes, amphibia, reptiles, birds, mammals); and even within this group are some forms which do not have a bony skeleton. This same phylum also has its central nervous system above or dorsal to the digestive tract, while in all other phyla the nerve cord is chiefly ventral in position.

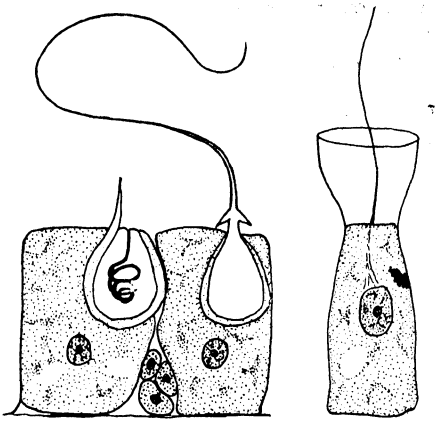


FIG. 3.—The distinguishing marks of two phyla. At the left, two stinging cells, one of them discharged, lodged among other cells of Hydra, the marks of a coelenterate; at the right, a collared flagellate cell, found only in sponges among multicellular animals.

Some characters are possessed by two or more phyla; in such cases there are other features which distinguish the groups. The coelenterates have only two layers of cells in their body walls, but so also do the sponges; these two groups are then distinguished by the collared cells, water pores, and horny or needle framework skeleton of the sponges, and the stinging cells of the coelenterates. The coelenterates have only one opening (the mouth) in their digestive cavity, but a cavity of this kind occurs also in the flatworms; the flatworms, however, do not have stinging cells, and have bilateral symmetry whereas the coelenterates are radial. A simple type of excretory system in which the primary function is performed by a "flame" cell, a hollow cell in which the excretions are moved along by the undulations of a flaglike structure, is found in both flatworms and rotifers; but these phyla are very different in most other respects.

Groups of lower rank are similarly marked. One class of mollusks (the snails) has a spiral shell (if any shell at all), another class has a shell composed of two hinged valves (clams, oysters), while a third class has arms bearing suckers (cuttlefishes). All members of the class crustacea (crayfishes, barnacles, etc.) respire by means of gills, even though some of them dwell on land; three other classes of arthropods (insects, centipedes and the caterpillarlike Peripatus) introduce air by fine tubes penetrating all parts of their bodies. These three latter classes have their distinguishing characters which need not be described.

Orders are distinguished in similar ways. Insects regularly have four wings; but the Diptera (flies) have only two, the hind pair being replaced with club-shaped balancers. In most insects having four wings, both pairs are used for flight; but in all beetles the front wings are hard covers which in flight are merely elevated to make room for the second pair to beat and at rest serve to protect the hind wings. Butterflies and moths all have on their wings shinglelike scales in which the color patterns are developed; some other insects have hairs or spines on the wings, but nothing like scales. Several orders of insects have sucking mouth parts (bugs, thrips), other orders bite (grasshoppers, beetles, dragonflies); the orders that are alike in this one respect are, of course, different in a number of others. Striking similarities and differences are also found in the type of development. All insects of the several orders to which grasshoppers, bugs and dragonflies belong undergo a development in which each stage molts its skin to form a larger animal differing from itself only slightly in structure. Butterflies, beetles, flies and bees, on the contrary, pass through three radically different stages—larva, pupa, adult—so unlike in structure that the uninitiated would suspect no connection between them.

These examples must suffice for taxonomic distinctions of the higher ranks in general. Were the entire animal kingdom surveyed, from phyla down to orders, even with no more minute analysis than that given above, almost the entire subject matter of a second-year course in zoology or comparative anatomy would be involved. To extend the same analysis down through families, genera and species, with their increasingly smaller differences, would draw upon scores or hundreds of specialized works, often of large size. The advantage of such analysis

would be too small to compensate for the labor. To the vertebrate animals, however, chiefly because their organization is similar to that of man and is consequently more or less familiar, it is worth while to turn for further illustrations.

Vertebrate Characters.—If certain groups be omitted from consideration, the vertebrates are characterized by an internal bony skeleton, a hollow nervous system located all on one side of the digestive tract (usually to be described as the upper or dorsal side), and gill slits opening from the throat to the outside or touching the outside wall in at least the developmental stages. These characters are found in no other phylum. In the fishes, the gill slits persist throughout life and between them the gills are developed as respiratory organs; the limbs are in the form of fins; the skin usually contains scales; and the heart consists of only two chambers. In the amphibia (frogs, toads, salamanders), gills are present and functional in the larval or tadpole stage and in some kinds they persist throughout life. The amphibian skin is devoid of any hard structures, and the heart has three chambers (two auricles and one ventricle). The reptiles never have gills in any stage, and the gill slits are open only in the embryo; in this respect they are like birds and mammals. The heart is generally three-chambered, though the ventricle is partially divided, and in crocodiles it is completely divided so that the heart is four-chambered. The body of a reptile is covered with scales or hard plates. Birds possess feathers, wings (functionless in some), a four-chambered heart, and air cavities in some of the bones, and are devoid of teeth. Mammals have hair, a diaphragm separating the chest from the abdomen, and a four-chambered heart. Embryonic development of mammals takes place as a rule within the body of the female, and the young are nourished with milk. The fishes, amphibia and reptiles are cold-blooded, while birds and mammals are warm-blooded.

The vertebrate characters which remain to be described are not advantageously referred to as taxonomic distinctions. Instead of pointing out the differences among various animals with respect to them, more is to be gained by emphasizing their similarities. The brain is an example. While some brains are long and narrow, others short and wide, some flat and others high, they all possess the same principal features. Cerebrum,

cerebellum, optic lobes, pituitary body, and the crossed optic nerves are readily discernible notwithstanding their variable forms.

The nerves that emerge from the central nervous system within the skull show likewise great similarity. They arise from the same part of the brain, and most of them pass to the same organs and serve the same function. The first of these nerves, counting from the front, is the nerve of smell, the second is the optic nerve, and the eighth is the nerve of hearing in all vertebrate animals. The third, fourth and sixth are distributed to the muscles which move the eye. The remaining cranial nerves—there are 10 of them in the lower vertebrates, 12 in the higher—go to various regions of the face, throat and organs of the chest, and among them there are some differences in both distribution and function in the several vertebrate classes.

The highly developed sense organs show equally great similarities. In the eye there is in all the same general arrangement. The eyeball may be of somewhat different shapes, but the transparent cornea in front, the iris and pupil, the lens, the retina and the choroid and sclerotic coats are present and in the same general relations to one another in all of them. The inner division of the ear, to which the nerve of hearing is connected, consists of an irregularly shaped body and three semicircular canals, two of them placed vertically but in different planes, the third set horizontally. Each canal of this membranous labyrinth has an enlargement near one end in all the classes of vertebrates described above. From the frogs to the mammals, there is, adjoining the membranous labyrinth, a cavity known as the tympanum, which is connected with the throat by a tube, and in which in all these classes are small bones which serve to convey the vibrations producing sound.

Any other system of organs could be used for similar comparisons, and would yield the same conclusions. Digestive systems in the bulk of the vertebrates consist of corresponding organs in the same order, with the appropriate glands pouring secretions into them at the same places. Excretory systems consist largely of the same mechanisms; muscles are arranged in much the same ways, are attached to corresponding bones, and serve mostly the same functions; blood vessels follow the same general courses, give off branches usually at the same points, and serve the same

portions of the body. It might be argued that these systems, in order to perform their functions, must be arranged in these ways, and that the fact that they are so much alike in the various vertebrates means only that they have certain things to do in relation to each other and are situated in the only places where these things can be done. This argument could not be applied, however, to the location of the endocrine glands. These organs produce secretions which, instead of being poured out through ducts, diffuse directly into the blood. In this liquid the secretions are carried everywhere, and there would be no necessity of having the glands located at any specific points. Yet the thyroid gland occurs always in the region of the throat near the front gill slits, from which place its secretion flows out to influence physiological processes in the remotest parts of the body. The pituitary, located always at the base of the brain, might be anywhere else and influence growth and the reproductive system equally well. The thymus develops always in the region of the gill slits, but in the adult extends, in the several classes of vertebrates, to various places in the neck region or upper part of the chest—far from the seat of its principal known and supposed effects. The reproductive organs produce endocrine secretions which influence secondary sexual characters from head to foot (combs, wattles, tail feathers and spurs of fowls, for example). The conclusion that these organs might be elsewhere and still serve the same purpose is not mere conjecture. It has been proved by grafting them into strange situations, or by introducing their secretions artificially at other points.

Internal Similarity with External Difference.—If experiments with the endocrine secretions show that a given function could be performed regardless of any particular anatomical arrangement, there are situations in which the tables are turned and many different functions are performed by essentially the same anatomical structure. A classical example of this relation, often described because it extends over a large number of well-known animals, is found in the fore and hind limbs of vertebrate animals. These limbs possess very similar skeletal foundations, but are externally modified in so many ways that they may be used for many different purposes. The human arm is rather simple and unspecialized, and its skeleton may be used as a starting point for comparisons. It is attached to the trunk through a shoulder

girdle composed, on each side, of a collar bone and a shoulder blade. The upper arm consists of one bone, the lower arm of two bones, and the wrist of a group of irregular small bones. Beyond these there are five chains of bones set end to end to form the body of the hand and the digits. Among the least specialized of the arms of other vertebrates is that of the frog. Its shoulder girdle contains a third bone on each side which forms the chief brace of the arm against the breast bone. The arm itself differs from the human arm chiefly in that the two bones of the lower

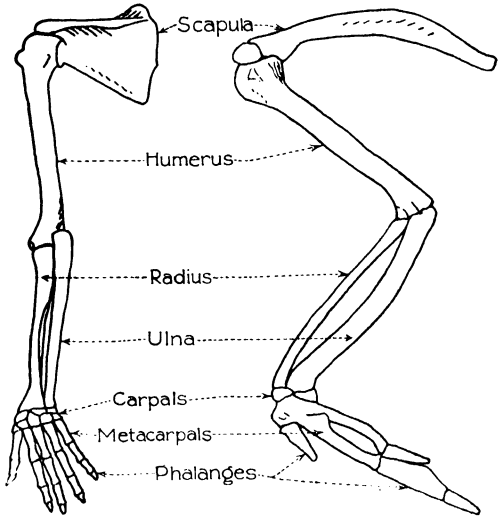


FIG. 4.—Skeleton of human arm and bird's wing, showing correspondence of their bones.

arm are fused side by side, the small bones of the wrist are less numerous, and there are practically only four rows of bones in the hand with somewhat different numbers of bones in them. In the sea turtles the fore limb is externally a long flat paddle, not divided in the flesh into separate fingers at the end. Yet, with the exception of the inflexibility of some of the joints, the bony structure within, even to the number of segments in the digits, is essentially the same as in many land vertebrates. The arms of whales are likewise flat and without separation of the digits in the flesh; but their skeletons differ from typical vertebrate arms almost only in the absence of a collar bone, the immovability

of the elbow joint, and an increase in the number of bones in the digits. In bats, the principal modification is the great elongation of the bones of the body of the hands and the fingers (except the thumbs) to form the framework of the wings. One of the bones of the lower arm is rudimentary; otherwise the arm skeleton is typical. In birds the wing is formed, not by an extension of the digits, but notwithstanding a great reduction of them. There are only three fingers (Fig. 4), and each of these has one or two fewer bones than the corresponding fingers of man. The expanse of wing thus lost is more than compensated by very stiff feathers. The only other striking difference between the bird wing and a typical vertebrate forearm is the reduction of the separate wrist bones to two. In the forefeet of horses there is only one well-developed chain of bones instead of the usual four or five, while

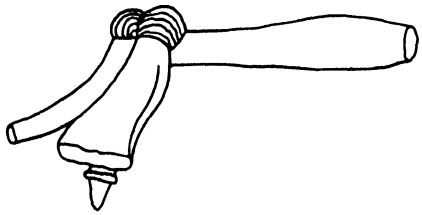


FIG. 5.—Vestigial skeleton of hind legs of some whales. The bones are not attached to the rest of the skeleton and no leg protrudes from the body.

two others are represented by the single splint bones on either side. The single toe in these animals is generally held to be in the interest of speed. In snakes the forelimbs are completely wanting, though the other skeletal characters show many resemblances to other vertebrates.

The hind limbs show somewhat fewer and less striking departures from the ordinary. In sea turtles and horses their modifications are of about the same kind and degree as those of the forelimbs. In most whales they are entirely missing, though in a few there are small bones (Fig. 5) embedded in the flesh in the pelvic region without any connection with the spinal column, which are usually homologized with the hip girdle. In most snakes, likewise, hind legs are wholly wanting. In a few (including the python and the boa), hind legs are externally visible only as clawlike structures scarcely protruding beyond the general level of the scales on the surface. Connected with these claws

internally are rudimentary bones representing the girdle and probably one or more of the leg bones.

Similarities between Embryos.—It is not only in adult structure that similarity exists between animals of different groups. Their embryos may show equally striking likenesses. Without inquiring at once how significant these various resemblances may be, it may be pointed out that they exist from the very beginning of development. Throughout the animal kingdom development involved in sexual reproduction begins with an egg, either fertilized or not, and the first step in development is the division of that egg. This cleavage continues, and in almost all cases results in a hollow ball of cells. One side of this ball is turned in (in very various ways) to form a double-walled embryo, in which, in most phyla, a third layer is soon split off or budded off. From this point on the similarities are striking only if comparisons be limited to one great group, and for this purpose the vertebrates are here selected. In all the vertebrates the nervous system arises early from two ridges formed on the outside of the embryo and later fused to form a tube below the surface layer of cells. From this tube, in all vertebrates, the eyes start as a protrusion on each side near the front end, and subsequent steps are very much the same in all. The ears start as a depression from the outside in the head region, resulting soon in a pear-shaped sac beneath the surface layer. This sac forms the membranous labyrinth with its three semicircular canals which have already been described as similar in the adult in all vertebrates. The digestive tract exists from the moment that the double-walled embryo is formed. The gill slits arise, in all vertebrates, as outpocketings of this inner cavity near its front end. The liver is derived in all of them from a protrusion on the under side of this cavity just behind the enlargement which later becomes the stomach. The pancreas is produced by two such protrusions on opposite sides of the digestive tract. The heart, in all vertebrates, begins as an S-shaped tube formed in the third layer of cells toward the ventral side. The excretory organs start as a series of tubes extending out from the body cavity; these later come to be associated with minute blood vessels, in almost exactly the same way in all vertebrates. The spinal column originates in all of them as a rod of cells just below

the central nervous system, around which later cartilage is formed and eventually bone is deposited.

The correspondence between different classes of vertebrate animals with respect to the development of their various organs is so close that college courses in embryology can easily be based in the main on one type. In some, it is the frog that furnishes the main laboratory study; in some it is the chick; while in others mammalian embryos are used. What is observed in one of these applies in general to the rest, with quite as much accuracy as the facts of adult anatomy in one animal indicate what is to be expected in the adult structure of other types.

Similar Embryos and Unlike Adults.—More striking because of their unexpectedness, though not more valuable as evidence, are similarities between embryos of animals whose adults are quite unlike. A classical case is the occurrence of gill slits in the embryos of all vertebrate animals, already referred to as one of the characters of the chordate phylum. In fishes, these slits persist, and in the adult are passageways for water flowing over the gills which form on the walls of the slits. In amphibia the slits persist through larval stages, and the adult stages of some, and serve the same respiratory function. In none of the higher classes of vertebrates (reptiles, birds, mammals), however, do the gill slits remain open to the outside. Some of them become structures not found in adult fishes, as the Eustachian tube, others close up without trace. No one would suspect, from the adult anatomy, the existence of gill slits at any stage in these higher groups. Adult anatomy is sufficient to indicate their kinship with the fishes and amphibia, but the occurrence of gill slits in the embryo is important confirmation of the relationship.

Occasionally embryos furnish the chief, and in some cases the only, clue to the relationships of animals. This is particularly true of parasites because the adult structure of such animals is frequently so degenerate as to obscure any similarities which may once have existed. Sacculina, a parasite attached to the under side of the abdomen of crabs, is a noteworthy example because it eluded classification so long. Sacculina is a rounded pulpy mass consisting mostly of reproductive cells, and having no other structural characteristics resembling any known group of animals. When some of its reproductive cells were allowed

to develop under observation until the larval stage was reached, it was discovered that Sacculina belongs to the group of crustacea commonly known as barnacles. Portunion, another parasite upon crabs, is shown by its developmental stages to be an isopod, a member of the crustacean order to which the sow bugs belong. Entoconcha, parasitic in sea cucumbers (relatives of starfishes), goes through an embryonic stage known as a veliger, of a form that is characteristic of snails. Embryos are so regularly similar in animals whose adults are similar that, when embryonic similarity is found in the absence of adult likeness, it must be regarded as sound indication of kinship, especially when the adult structure does not indicate different affiliations.

Vestigial Structures.—Degeneration less extreme than that exemplified in the parasites just mentioned may result in vestigial organs. While in Sacculina all organs represented in the embryo are lost to the adult except the reproductive organs (which show no characteristic structure), and in numerous other cases certain organs of the embryo are wanting in the adult, there are many instances of structures whose embryonic start is ordinary but whose later development is retarded. Such organs are often so much reduced that they are functionless, and then are known as vestigial organs.

Examples of vestigial organs are numerous. The vermiform appendix and caecum in man start in the embryo in as conspicuous a way as they do in kangaroos or rabbits, animals which in the adult stage possess these structures very well developed. The uselessness of the appendix in man is attested by its frequent removal without ill consequence. While surgeons sometimes hesitate to remove it in very young children because of a possible developmental function, such significance has never been demonstrated. The human coccyx consists of those vertebrae below the pelvic girdle, and corresponds to the tail vertebrae of other mammals. It is much reduced in size, and is immovable, though in some individuals rudimentary muscles are found adjoining it in the same position as the muscles that move the tail in the tailed mammals. In rare instances the coccyx is overdeveloped and produces a taillike projection. In the human embryo of an early stage it is present in as well-marked a form, the curved posterior tip of the body, as in the embryo of a tailed mammal. Ear muscles are present in man, though not all people are able

to operate them. The slender red crescent at the inner corner of the human eye begins in the embryo in precisely the same way as does the eyelid of a bird. Instead, however, of becoming functional, it is replaced by two lids of a totally different type.

The wings of birds of several kinds suffer eclipse in the course of development. Those of the ostrich are too small to be functional, while the wings of the New Zealand kiwi are completely concealed by the plumage. In the early embryos of these birds there is no suggestion of the impending retardation of wing development. In the dodo, which is now extinct but was known on the island of Mauritius as late as the year 1681, the wings were correspondingly reduced; and in the moas of New Zealand, which are known only from recovered bones, no wing bones have ever been found. In these latter two birds there is no evidence regarding the embryonic development of wings.

The hind legs of whales are missing, except for small bones (Fig. 5) in some of them wholly embedded in the flesh and unattached to the spinal column. A few snakes have corresponding remnants of hind legs. The splint bones at the sides of the feet of horses recall the ancestral condition in which there were at least four toes, according to the fossil evidence described in another chapter.

Hundreds of such vestigial structures are known. They are not any better as evidence of kinship than are well-developed homologous organs. They effectively dispose, however, of any supposition that embryonic development proceeds directly by the shortest route from the egg to the adult form. This is important in the interpretation of embryonic likeness, since it cannot be maintained that embryos are alike merely because development has to arrive at somewhat similar end products and must run everywhere the same course in order to do so.

Similarities of Physiology.—While anatomy is the oldest of the biological sciences, knowledge of physiology is likewise of very great age. The general features of the functions of the more obvious organs are well known for a considerable number of animals, particularly among the vertebrates. Domestic and laboratory animals furnish the bulk of the knowledge already gained regarding physiological activities. Little would be gained here by reciting what the facts of physiology indicate regarding the kinship of animals, for they parallel to a great extent the

evidence from anatomy. The organs of the digestive tract produce in the main similar enzymes in various vertebrate animals. The parts of the central nervous system perform, so far as they have been adequately tested, approximately the same functions. The nerves not merely are distributed to the same parts of the organism in different vertebrates, but serve chiefly the same ends. The functions of these organs must be in part determined by their structure and relation to other organs. Thus, an efferent nerve probably differs little in fundamental function no matter to what organ it leads; but the end result of its activity varies greatly according as it innervates a muscle or a gland. A voluntary muscle presumably contracts by means of the same physical and chemical properties no matter where it is located; but the movement effected by it depends on the bones to which its ends are attached. In this sense, and to this extent, physiology parallels anatomy and furnishes no new evidence regarding homology.

There are some physiological properties, however, which are not obviously associated with or dependent upon anatomy. Similarities between different animals with respect to such qualities should possess all the value as new evidence that an independent anatomical feature of the adult or embryo would possess. Such physiological properties may be discovered in the blood. This statement does not refer to the similarity of the blood cells, the hemoglobin content of some of them, or the chemical composition of the blood as ascertained by ordinary chemical analyses. Such similarities are indications of kinship, but are omitted because each of them can be discovered by essentially structural studies. The properties which possess evidential value of an independent sort are those revealed by serological tests. The details of method need not be described. By injecting into the blood stream of one animal the blood serum of a different kind of animal the blood of the former may be gradually rendered immune to the latter. This is done by the production of antibodies. The presence of the antibodies is shown by the production of a white precipitate when the serum of the immunized animal is mixed with serum from the kind of animal to which it is immune. There are degrees of this precipitation reaction, indicating degrees of similarity in the types of blood mixed. On the basis of such tests it has been shown that

human blood has no close similarity to that of any other vertebrate except in the group of primates. Within the primate group, human serum is most nearly like that of the anthropoid apes. The apes are followed, with lesser degrees of similarity, by the Old World monkeys, the New World monkeys, and the lemurs.

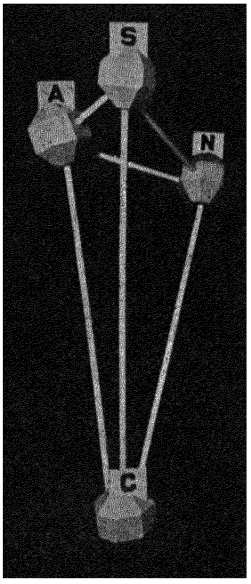


FIG. 6.—Model of the degrees of kinship of four salamanders, Amphiuma (*A*), Siren (*S*), Necturus (*N*) and Cryptobranchus (*C*) as determined from blood tests. (*From Boyden and Noble, American Museum Novitates.*)

Many precipitin tests have been made in other groups of animals. Boyden and Noble (1933) have illustrated the results of comparison of four genera of salamanders by the model shown in Fig. 6. The lengths of the rods connecting the polyhedra represent the degrees of relationship among the salamanders, a long rod meaning distant relationship, a short rod close kinship. Amphiuma, Siren and Necturus are rather closely related to one another, while Cryptobranchus is distant from all of them. Cryptobranchus has long been regarded, on anatomical and other grounds, as a primitive form. Thus the serological tests are in agreement with the morphological evidence.

Summary.—In all the instances related in this chapter, similarity can be reasonably attributed to only one cause, namely, heredity from a common ancestor. Whether the likeness be exhibited in adult structure, in embryonic structure or processes, or in physiological properties, there is no other known way of attaining it than by community of descent. Such resemblances are more impressive if they are independent of other parallelism, or if they occur in unexpected places, but are not then necessarily of greater value as evidence. Their greatest testimonial worth lies in the fact that everywhere they point to the same conclusion.

If animals of different taxonomic groups have, as their similarities seem to show, sprung from the same ancestors, then evolution has taken place. For along with their likenesses which prove kinship, they also have differences which must have arisen somewhere in the line of descent.

CHAPTER III

GEOGRAPHIC DISTRIBUTION AND THE TIME AND PLACE OF ORIGIN OF SPECIES

> . . . the science of geographical distribution depends essentially on a belief . . . that all animals are genetically connected one with another, and that the existing forms have originated from earlier kinds by some mode of evolution. R. LYDEKKER, 1896.

The qualities of organisms are shown in the first two chapters to be more in keeping with an evolutionary rise from common stocks than with totally independent beginnings. Apart from these qualities is the arrangement of species over the earth's surface, which likewise, as will be seen, is more intelligible as a consequence of a gradual unfolding than as a result of unrelated origins. The facts of geographic distribution are enormously complicated and are much more readily understood if approached with the evolution concept fully in mind; even when the origin of species one from another is taken for granted, many curious and important puzzles are found in their present spread. It would be logical to proceed in this manner, even at the risk of appearing to argue in a circle, if it were desirable to devote, at once, the necessary space to the subject; for, if evolution were shown to account readily for the peculiarities of distribution, and independent origin of species failed to explain them, the facts would be strong evidence of the former explanation. In much less space, however, may be demonstrated two of the general conclusions to be drawn from distribution, which directly support the view that species have evolved from common stocks. These conclusions are that species have originated at widely different times, and that their places of origin are geographically far distant from one another.

In whatever manner life originated, that event must have had a time and a place. Those views of the nature of the first living matter which are based on fundamental physics and chemistry, and on logical deductions regarding the probable origin of the

earth, have postulated an origin of life at some particular stage in the earth's development. Though life might have come into existence a number of times independently, the repetitions must all have occurred within a suitable period. Beliefs regarding the beginnings of life which rest on tradition have postulated a monumental work of creation in which the whole living world was given its start. In either case, the start must have been made somewhere; and even if there were several origins separated by not too long periods of time, each one must have occurred at some particular place.

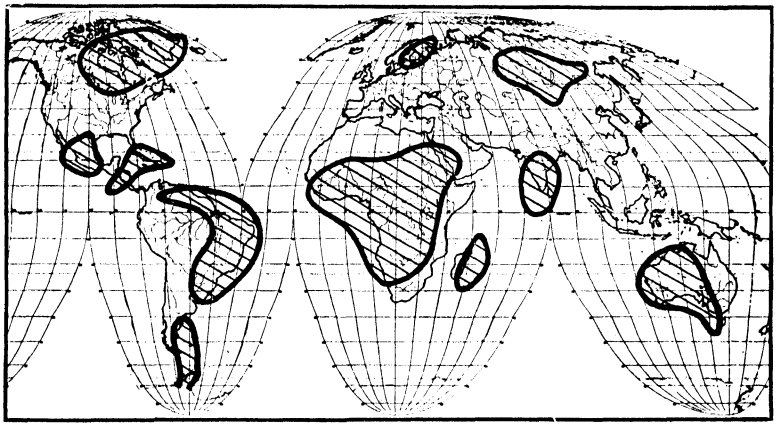


FIG. 7.—Map of the world showing the continental nuclei. In each of the areas marked are lands that have never been under the ocean, although in most of them not all the land has been thus continuously dry.

If it be supposed in these origins that each species was at once constituted in its present form, that fact should have an important bearing on the present distribution of the species. A marine species would have had an open highway, inasmuch as all oceans are in communication with one another; but it would have been hampered by its reactions to different temperatures, to mechanical agitation of the water, to light (which penetrates in significant amounts only a thin surface layer of the oceans), and to the nature of the bottom materials. It would have been restricted also by the presence or absence of food organisms which likewise reacted in certain ways to all or some of the foregoing factors. If species were from the first what they are now, they possessed all these reactions and must have been guided by them. Not-

withstanding the connections between all oceans, therefore, marine species would not have been free to spread everywhere.

A land species would have been restricted still more, since land conditions are much more variable, and since very few terrestrial animals can readily cross arms of the sea. The geological evidence goes to show that continents and oceans have long been roughly where they now are, though with many partial subsidences and emergences of the continents. In the midst of all the changes to which the land was subject, a number of land bodies have remained above water ever since the time at which, presumably, living things could first have existed. One of these continental nuclei was in Siberia and Mongolia, one in Canadian North America, one in Australia, one in South America, one in Africa, and smaller ones in Mexico and Central America, northwestern Europe and elsewhere (Fig. 7). The precise locations are not important here; a land species originating early must have originated on one of them or on the somewhat larger area including it and, wherever it be at the present time, must somehow have traversed the distance between the two places. Its present location could hardly escape being determined in part by its place of origin. Let us see how well the present locations of species fit these suppositions.

Location of Species on the Earth.—No very extensive knowledge of the land fauna and flora of the world is necessary to show that most species are limited to certain definite regions. Most of them are not even widespread, and almost none of them occupies a whole continent. The most striking examples of this restriction are found on islands more or less distant from other bodies of land. Thus, of the species of plants found in the Hawaiian Islands, 83 per cent occur nowhere else in the world. Several thousand species of insects occur there, and most of them are limited to this archipelago, while one whole family of birds including 60 species occurs only there. The aye-aye occurs in Madagascar and is so different from any other species that it has been constituted a separate genus. Of some 260 species of birds in Madagascar, half are found nowhere else, many of them belong to genera peculiar to that island, and some even to families that are limited to it. Forty per cent of the species of plants and 96 per cent of the reptiles on the Galapagos Islands live only there. When Charles Darwin visited the islands, a number

of the islands had each its peculiar species of tortoise, but these are now on the verge of extinction. Forty-three species of birds are known only from Jamaica, 74 species only from the Bismarck Islands, one wingless bird (the kagu, allied to the bitterns and cranes) only from New Caledonia, one species of puffin only from the Cape Verdes. Fifteen species of Greenland plants are endemic, as are also about three-fourths of the 1000 species of plants in New Zealand. Not all islands are so distinct, for in Java only a few of the nearly 500 bird species are peculiar, and not a single genus is limited to it; but on the whole, the more isolated islands are characterized by many species not existing elsewhere. (See Fig. 8 for the location of some of these islands.)

The larger bodies of land also possess their peculiar species, but the areas are not so sharply marked off nor so readily indicated. The yak is confined to the high mountains of Central Asia; South Africa alone has the secretary bird and two insectivores; only in tropical South America are there prehensile-tailed monkeys. While, as is more particularly pointed out below, species vary greatly in the amount of the earth's surface which they occupy, no species is found everywhere in the world, and most species are found only in a very small fraction of it. The important point here stressed is that, with very few exceptions, it is not the same fraction for any two species.

Almost as important is the fact that there are regions from which certain animals are excluded. When made concerning species, this statement is only a corollary of the preceding paragraphs. When it refers to larger taxonomic groups, it has added significance. There is no species of bear in Africa, for example. New Zealand and the Hawaiian Islands rival Ireland in their snakelessness. In the latter islands there are only seven species of reptiles of any kind; these are skinks and geckos. Java, which is not particularly individual in its fauna, in that it has most of the 176 species of mammals found in the Malay Archipelago, nevertheless does not contain elephants, tapirs, or bears. The Antilles, Madagascar and the Malay Islands east of Borneo and Java lack cats. Oceanic islands in general are very poor in mammals, their principal representatives of this group being rodents and bats.

Meaning of Geographic Position of Species.—How can these peculiarities of distribution have come about? The occurrence

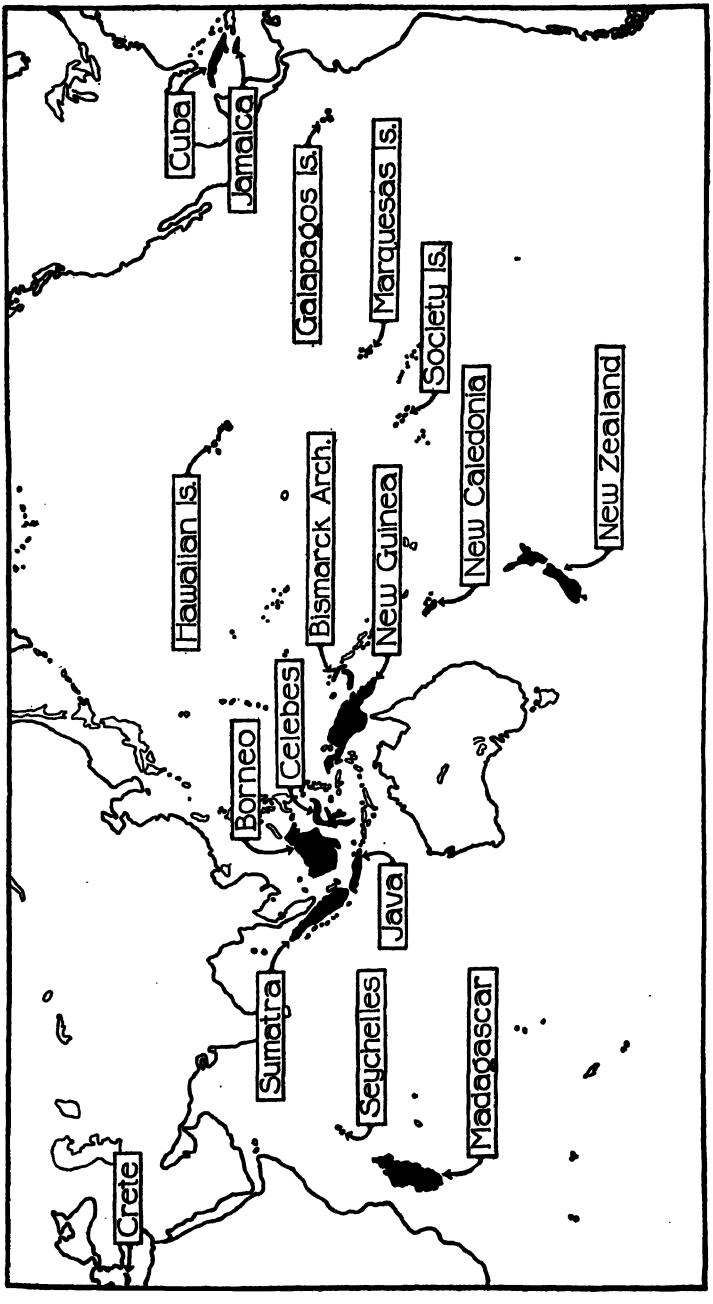


FIG. 8.—Map showing the locations of some of the islands mentioned in the text.

of a species only on a small group of islands might, if it were an isolated instance, conceivably be regarded as the result of extinction from the major portion of a once much larger range. But when many species are limited to a single small area, this explanation must almost certainly be rejected, since the original areas occupied by the several species must have been very unequal, and it is scarcely possible, purely as a matter of chance, that the extinction would have blotted out each of them from all regions except the small one which they now occupy in common. The Hawaiian group of islands may serve as an example. They are of volcanic or coral origin, and have never been connected with one of the continents. If animals of all kinds arose in the form in which they now exist, it would fit the Hawaiian situation best to assume that land species, or at least some of them, originated on a Central American land nucleus. From this center they should have spread. It is a little peculiar, however, that they should have spread chiefly to the Hawaiian Islands, and still more peculiar that so few of them remained in Central America. While climate and other conditions may have changed so as to drive some species out of Central America, and while accidentally a few of these might have arrived at a hospitable situation only in Hawaii, it strains the laws of chance to have hundreds of species suffer the same fate. No help in solving this puzzle is given by assuming that the islands have not always been isolated, that is, that they were part of the mainland once; the chance that the animals would have migrated only to this one region before separation of the islands from the mainland is too small to consider. Nothing is to be gained by assuming that one of the supposedly few origins of life occurred in the Hawaiian Islands and that the spread took place from there, for then the peculiarities of Central America in *not* having so many of the Hawaiian species, and the individualities of the West Indian islands and other regions are left unexplained.

An approach to an explanation of the peculiar distribution of species may be made if it be assumed that the origin of land forms was not limited to a few, or even to all, of the land nuclei of the earth. An origin of species in the Canadian center can not explain the occurrence of species in Madagascar and Africa which are unlike any in North America. An origin of species in Mongolia cannot explain why there are few or no forms common

to Asia and South America. Assuming several origins of species at different places is, however, only an entering wedge. To explain all the peculiarities of distribution it seems necessary to assume that practically all habitable parts of the earth have witnessed the origin of species. The species of the Hawaiian Islands are most of them peculiar to that area because they originated there and have not been able to spread elsewhere. Those species which are common to the islands and the mainland could have originated in either or any of the places where they are now found, and have been in some way transported to the other portions of their range. Snakes may be assumed to be absent because no snake species originated in Hawaii and none has been able to cross the water barriers. The species of birds and mammals now found only in Madagascar have probably never been anywhere else; they originated there and have not succeeded in passing beyond that island's confines. In like manner the peculiar New Zealand species may be supposed to have arisen in or near New Zealand, those of the Bismarck Islands, New Caledonia and the Cape Verdes in or near their present ranges. With respect to species limited to portions of the continents it is not so clear that the species could not have migrated overland, and be now considerable distances from their places of origin; and yet, it is questionable whether a species that had migrated far could be the same species as formerly, though in raising this question one is taking for granted the evolution process which it is the purpose of this discussion to substantiate.

In general, it seems more reasonable to assume that, on the whole, species originated somewhere within, or not far distant from, their present ranges. This is a general statement and does not preclude the possibility that an occasional species has migrated widely and disappeared from its original haunts. Such an occurrence would generally depend upon a climatic or other change which rendered the original area unsuitable, and would require presumably a long period of time. Allowing for even a considerable number of such migrations of all individuals far from the places of origin of their species, it must still be regarded as a highly probable generalization that species are now mostly around or near their starting points. Zoogeographers have often asserted that the present distribution of an animal affords no

clue to its point of origin. This statement is always made, however, of taxonomic groups of higher rank than the species. It is said that the fact that marsupials are almost limited to the Australian region and South America does not mean the marsupials originated in either of these continents. This is true, but the marsupials are an order. No student of distribution would maintain that any modern species of marsupial were among those in existence when first there were marsupials. All that is meant when it is said that marsupials are not now where they originally were is that the first mammals possessing the characteristics that mark off the marsupials from the other groups of mammals probably existed in one of the northern continents.

If species are at present not far from their places of origin, and species have sprung up all over the earth, it is clear that any nonevolutionary origin of kinds of living things must be somewhat different from the methods that have been proposed. But scattered origins of species are not only consistent with an evolutionary method of production, they are a necessary consequence of it.

Regional Similarities of Species.—Were the peculiarities of distribution merely that each species has its own particular niche, to which it could not have traveled without occurring in various regions along the route of migration, it still would be possible to imagine that the origins of these species were all independent of one another. Whatever agency caused species to arise would only have had to operate in many places, be that agency evolution or anything else. There are many facts, however, which seem to require a relation of some sort between the origins of different species. General similarities among species occupying neighboring areas imply such relations. The island of New Guinea has two genera of marsupials peculiar to it, but, as marsupials, they resemble the characteristic mammals of Australia and are correspondingly unlike anything in Asia. New Zealand likewise exhibits similarities to Australia, both in its animals and in its plants. The Bismarck Islands, in turn, have birds resembling those of their near neighbor New Guinea. The island of Celebes, the poorest in animals of any of the major units of the Malay Archipelago, has the babirusa, the black-crested baboon and the dwarf buffalo which are not only peculiar to the island but are closely similar to forms found only on three

of the neighboring small islands. One family of plants including a hundred species on the Hawaiian Islands is also well developed in South America, but less so in other regions. On the Hawaiian Islands some 970 different kinds of snails (whether they be called species or varieties is not very material) are found. To a large extent these forms occupy different valleys or groups of connecting valleys, and there is a gradual regional change among them. The species or varieties in any group of neighboring valleys are more like one another than they are like those of more distant valleys, and between two kinds distant from and unlike one another there is often a more or less steady change in the characters of the varieties over the intervening valleys from one extreme to the other. It is generally true that two separated areas which have many species in common possess also species, which, while not identical, are more closely similar to one another than any of them are to species in more distant areas. This is true of the Marquesas and the Society Islands, it is true of the Cape Verde Islands and the African mainland, and, at least with respect to plants, of Greenland and the North American continent.

It is not only the islands that show these similarities; the continents also have their faunal affinities. Australian animals are more like the South American, the North American animals more like those of Europe and Asia, than like those of other continents. The wapiti of the Rocky Mountains, unfortunately called an elk though not at all like the European mammal first called an elk, is very similar to the European stag, and still more like the Asiatic stag, the three forms being different species of the same genus (Cervus). The American moose, which is the sort of animal called elk in Europe, is so similar to the Scandinavian elk that they can almost be regarded as the same species. The caribou or reindeer of northern North America is very close to the Lapland reindeer. The American bison and European bison are two species of the same genus.

Just as significant are those differences between continents which are accompanied by great similarities within each continent. The monkeys of South America frequently have prehensile tails, but no Old World species has this character; the Old World species, except the manlike apes, have naked callosities on the buttocks not possessed by any American species. North and South America have many species of rodents, but the various

species of ground squirrels, marmots, prairie dogs, beavers, meadow mice, jumping mice and pocket gophers are all in the northern continent, while almost all of the porcupines (six families, including 29 genera) are South American. All of the sloths (two families), those curious slow-moving, long-limbed, hook-footed mammals which hang back downward from the branches of trees, are in tropical America. Two other families, the anteaters and armadillos, which are similar enough to sloths to be included in the same order, are likewise found only in tropical America, with the exception of one species, the nine-banded armadillo, which got as far north as Texas.

Congregation of closely similar species in limited parts of a single continent is very common. The several species of moles which are enough alike to be regarded as belonging to the genus Scapanus are all in the Pacific coast states, while another group of species differing from the western forms so much as to be excluded from the genus Scapanus but similar enough among themselves to be another genus (Scalopus) is found scattered through eastern North America. A number of species of chipmunks whose similarities are recognized by putting them all in the genus Eutamias are all in western North America, while varieties of the genus Tamias are all eastern. All zoogeography is marked by such examples. It is the rule that species much alike shall be near one another; any separation of species similar enough to belong to the same genus into two or more regions with wide gaps between, thus causing discontinuity of the genus range, occasions comment on its rarity and speculation upon the way in which it came about. The genera constituting a family show the same tendency to occupy the same general region of the earth, though the family ranges are larger and discontinuity is not so rare.

Sometimes the similarities are not what would be expected on geographic grounds, for the fauna of Madagascar is most similar, not to that of its near continental neighbor Africa, but to that of Asia, the gap being bridged over by the Seychelles Islands whose animals are similar to those of Madagascar. The animals of New Guinea, as pointed out above, are similar in general to those of Australia, but quite different from those of almost equally near islands to the north and west; and the fauna of Sumatra is more like that of Borneo than like that of its nearer neighbor

Java. These peculiarities all have their special explanations, which it is beyond the province of the present chapter to discuss; the phenomenon to be emphasized is that regions geographically near one another so frequently show greater similarities of their living forms than usually exist between more distant areas.

Were species entirely independent of one another in their origins, such regional similarities could hardly exist. There must be some relation, genetic or otherwise, between species so located. The genetic relation is the only one that has ever appeared to be a satisfactory explanation. Origin of species by evolution from other species is not only in agreement with such geographic collections of similar species, it would almost necessitate their existence. A group of species derived, in a given part of the world, from a common stock, from which each came to differ, at the time of its origin, in a few minor respects, could not well avoid showing among themselves greater similarities than any existing between them and species developed from an unrelated stock.

Is Age of Species Indicated by Spread?—Among the numerous species which are limited to one well-defined portion of the earth are not a few whose areas are remarkably small. These diminutive ranges are especially impressive when they are compared with others which extend over most of a continent, or into two or more continents. Taking the earthworms of Canada and northern United States, which are of the same species as those of Europe, as a not extreme example of the great size to which a range may extend, let us examine some of the smaller areas. One species of violet is known from only a few square yards in the Hawaiian Islands. Several species of trees peculiar to this archipelago are found only on a 56-acre tract surrounded by lava. One of these species was at first described from only a single specimen, but more are now known. The lava strongly suggests that the range was once somewhat larger, but it can never have been very extensive. A flightless cormorant is found only on Albemarle Island of the Galapagos group. The smallness of these island ranges is not usually difficult to explain, especially where a whole island is occupied, since the sea is an effective barrier against migration of many species. For such species, if their origin within their present ranges be accepted, smallness of area must usually follow. It is otherwise, however,

on the continents. There is a species of lizard which is found only in the southern peninsula of Greece, with perhaps some representation on the island of Crete. Another species of the same genus (Lacerta) occurs in its typical form all through central Europe and the Mediterranean states, while if its varieties be included the species extends into western Asia and northern Africa. A species of toad is found only in Texas, while another species of the same genus (Scaphiopus) occurs in most of the states from the western plains to the Pacific coast. A species of turtle is limited to southwestern Texas and the adjoining portion of Mexico, while another species of its genus (Gopherus) ranges through almost the whole of the southern states. A species of tree frog lives only in the valley of the Potomac and York rivers in Virginia and New Jersey; another species of the same genus (Hyla) has spread over the eastern half of North America.

The differences between the sizes of ranges in the last several examples can hardly be explained by barriers. Probably none of these species has reached insurmountable obstacles to its migration on all sides. One of the turtles mentioned as occupying a small range is a desert species, but apparently has not occupied all the desert areas directly open to it. So far as can be ascertained there is nothing peculiar about the small valleys occupied by one species of Hyla that would account for the absence of that species from other valleys, and the road to those other valleys is probably not blocked. Such statements have to be made with caution, for the physiological properties of animals are never fully known, and there may be undiscovered features of their environments that could act as barriers. Yet the safest way to use evidence is to accept it at face value after the most careful study, and then attempt to discover what it means. The evidence is that some species have smaller ranges than others that are very similar to them, when there is nothing either in the animals themselves or in the environment which would appear effective in preventing the enlargement of the small ranges.

The principal other conceivable reasons for smallness of range are (1) that the species is young and has not had time to spread far, (2) that its powers of multiplication or migration or both are limited, and (3) that it is approaching extinction, being perhaps very ancient. The last possibility should be relatively uncommon, because extinction is apt to come about rather suddenly

after a species has got down to small numbers of individuals. Approaching extinction is apt to be recognizable, also, by the absence of any very similar species near it. For example, a lizard species of the genus Cricosaura, which is held to be archaic, is found only on a few hundred acres of coastal plain near Cabo Cruz, Cuba. No similar lizard species is anywhere near. Restriction of range due to the youth of a species and that due to low fertility or sluggish migration are not easy to distinguish. Seldom is enough known about the properties of a species to say which of these two is the governing factor. In one instance it is possible to eliminate age as the principal factor of spread, namely, in two species of shepherd's purse (genus Bursa). From certain facts regarding chromosomes and the inheritance of the shape of the seed capsule, to be described in a later chapter (page 90), it is practically certain that one of these species was derived directly from the other. The derivative, which would be the younger species, is, however, spread over much of Europe and North America, while the parent species is limited to portions of Europe. The new species in this instance is simply the more successful of the two. Among the Hylas referred to above, it appears to be thought by herpetologists that the Potomac and York species is young, though it is impossible to be sure.

The idea that size of range depends on the age of the species, that is, on the duration of its process of spread, was emphasized by Willis under the name "age and area hypothesis" in 1922, but it is at least a century old. Considerable support for the theory is found in the distribution of many different types of living things. Unfortunately, however, for the use of this support here, it relates largely to taxonomic groups higher than species. It has been the purpose in the foregoing discussion to employ only species for contrast, since the use of genera or families or orders would necessarily involve to some extent the view that higher ranking groups had evolved from lower and would savor of arguing in a circle. The evidence that would most conclusively show area to be dependent on age would be to find deeper, hence older, fossils of some wide-ranging species, and only shallower fossils of some closely circumscribed species. Paleontologists are not blest, however, with abundance of fossils belonging to living species. Only a few fossil forms very closely resemble modern animals or plants, and it is very unlikely that even in these

few cases the fossil type could be regarded as of the same species as the modern, if its anatomy were sufficiently preserved to make an adequate comparison possible. When larger groups are used, there is some evidence that those having the deeper fossil representatives are on the whole the more widespread; but these comparisons to be valid must rest on the assumption that all members of the group are genetically related to each other, which is an evolutionary assumption.

Time of Origin of Species.—Whether size of range furnishes valid evidence of the age of a species is not, however, a crucial matter. There are other indications, the general nature of which has been pointed out in this chapter, that some species are old and others young. The implications are that at every period of the history of life since its early stages there have been young and old species. That is, species have been arising at frequent intervals throughout that time. This situation fits an evolutionary origin admirably. If species came into existence by modification of some individuals of an older species, these groups would necessarily be of unequal ages. The whole evolutionary scheme would require the development of new species, one after another, on a magnificent scale. Contrasted with this, nonevolutionary hypotheses regarding the inception of species have included the assumption that species all arose within a comparatively brief period. These nonevolutionary hypotheses could be modified to recognize differences in time of origin, and proposals have occasionally been made that the hypotheses be thus modified. Such proposed changes in the nonevolutionary theories of the origin of species do not serve to unify the whole process because they do not have logical connections with one another. They may make it appear unnecessary to abandon the creational view, but they do so only by substituting for one general theory a number of particular theories, all equally lacking in rational support. Reasonable connections exist between phenomena in all other fields of biology, and it seems hardly likely, a priori, that they are lacking in the origins of species.

CHAPTER IV

FOSSILS SUGGEST EVOLUTION

> Thus, on the theory of descent with modification, the main facts with respect to the mutual affinities of the extinct forms of life to each other and to living forms, seem to me to be explained in a satisfactory manner. And they are wholly inexplicable on any other view.
>
> CHARLES DARWIN, 1859.

To one who at the present time inspects the known fossil animals and plants in relation to the geological age of the deposits in which they are found, it would seem that these fossils must very early have suggested the evolution of species from other species. Actually, however, they have not been historically in the lead in evolution theory. Lamarck, the earliest avowed evolutionist of any great significance, arrived at his concept of evolution largely on other grounds. Though he studied fossils and used them to support his evolutionary views, that development came late in his life and was a consequence rather than a cause of his advocacy of evolution. Darwin, a later most important contributor, leaned heavily on other considerations. While in his "Origin of Species" fossils are employed, his discussion of them is introduced by a chapter entitled On the Imperfection of the Geological Record, which seems to indicate that he felt the contradictions offered by fossils to his theory more keenly than he felt their support. This discussion is preceded by chapters on artificial selection, the effects of domestication, classification, population increase, instinct, the physiology of variation and hybridization, indicating presumably a greater reliance placed on these as evidence or as material influences. Finally, Cuvier, who was among the great students of fossils at the time when the evolution doctrine was being seriously advanced, saw fit to oppose that explanation vigorously.

In the light of modern knowledge of fossil forms and of stratigraphy, it may seem strange that these extinct organisms were not more extensively used in the early evolution discussions. It

must be remembered, however, that knowledge of them a century or a century and a quarter ago was very meager compared with that of the present time. Moreover, geology was itself then only struggling toward a rational interpretation of earth features. The uniformitarian doctrine, according to which geological processes have been of the same general sort through long periods of the earth's development, and which has been one of the major unifying factors in geology, was first proposed and generally rejected in the eighteenth century, and required the great weight of Sir Charles Lyell's authority to establish it well along in the nineteenth century. Lyell at first adhered to the view that species are permanent, and later when he adopted the evolution concept it was under the influence of Darwin's studies, with which he was acquainted long before their publication in the "Origin of Species."

At the present time fossils constitute one of the most convincing indications of the origin of species at different periods, and of the general course which evolution has taken if the assumption be made that all forms, or at least large groups of them, are genetically connected with one another. Contrary assumptions have sometimes been made but appear to be untenable, for reasons to be stated later. Because of this obvious relation of fossils to evolution ideas a brief review of the sequence of extinct animals and plants is desirable.

Geological Periods.—In order to refer intelligibly and briefly to events in geological time, it is most convenient to employ the names of periods which are naturally marked off from one another by events that plainly occurred in the development of the earth. When stratified rocks, which must have been deposited under water, are sheared off obliquely and are covered by totally different stratified material set at a different angle, it is apparent that the construction of this portion of the earth took place during two periods of submergence, separated by a period of elevation above water accompanied by erosion. When the masses of dissimilar stratified rock contain strikingly different fossil forms, it appears certain that a considerable time elapsed between the submergences. On the assumption that extinct forms lived in situations similar to those in which the modern organisms most like them live, it can often be concluded that periods were characterized by mild, or cold, or wet climate. On

the basis of such differences geological time has been divided into periods, epochs or eras, as shown in the table below. No attempt is made, in arranging this chart, to bring divisions of equal rank into the same column. For the most part they are so arranged, but the table is purely for convenience of reference, and should be used constantly with the succeeding accounts, until the order of the periods is learned. To take advantage of the similarity of such a table to the column of rocks and other deposits, the oldest periods are placed at the bottom, the most recent at the top.

Geological Time					
	Psychozoic				Recent
	Cenozoic	Quaternary		Glacial	Pleistocene
		Tertiary		Late Tertiary	Pliocene
					Miocene
				Early Tertiary	Oligocene
					Eocene
	Mesozoic	Late Mesozoic		Cretaceous	
				Comanchian	
		Early Mesozoic		Jurassic	
				Triassic	
	Paleozoic	Late Paleozoic, or Carboniferous		Permian	
				Pennsylvanian	Tennesseian
				Mississippian	Waverlian
		Middle Paleozoic		Devonian	
				Silurian	
		Early Paleozoic		Ordovician	
				Cambrian	
	Proterozoic	Algonkian		Keweenawan	
		Neo-Laurentian		Animikian	
				Huronian	
	Archeozoic	Paleo-Laurentian			

Earliest Life.—Formations regarded as Archeozoic are known chiefly in northern North America and Europe, in China, and in Australia. Fossils are unknown in these formations. The occurrence of graphite in them is, however, taken to mean that simple plants capable of carrying on the carbon cycle then existed. Enormous masses of limestone of Archean age also probably owe their origin to secretion by plants; for, though limestone may be deposited by chemical action, deposits known to be formed in this way are of local occurrence and are derived from earlier limestone. In the Proterozoic there are unquestionable fossil animals and plants. Almost all the plants are algae.

some of the colonies of these found in limestone being a foot in diameter. A vascular plant, which is considerably more complex than the algae, found in Czechoslovakia, has been doubtfully assigned to Proterozoic time. Among animals, siliceous sponges of that age are exposed in the Grand Canyon, and burrows believed to be those of worms have been found in Algonkian sandstone in Montana. Shells of the protozoan order Radiolaria have been found, and Foraminifera are believed to have existed though their shells have not yet been identified. Glacial till in Canada in the Huronian formation, and in the Australian region in somewhat later deposits, indicate cold climate at least twice during the Proterozoic.

The Cambrian Outburst.—Compared with the paucity of fossils in the Proterozoic deposits, the Cambrian has the appearance of pouring out a deluge of living things in great variety. As if suddenly, all the principal phyla of animals are represented in deposits of this period. Geological periods are all inconceivably long, and Cambrian was probably one of the longer ones; but even after making allowance for this great span of time, the occurrence in it, for the first time, of many hundreds of species so diverse as to belong collectively to most of the phyla that have ever existed is an apparently abrupt beginning. The abundance and variety of life are rendered even more impressive by the consideration that almost certainly only a small proportion of the existent types were fossilized. That Cambrian life was not the sudden eruption which it appears to be is, of course, the view held by biologists in general, for it is regarded as the result of a long period of unrecorded evolution. Since in the main only organisms with hard parts are abundantly preserved, and since by an evolutionary origin the earliest living things can hardly have possessed such hard parts, the assumption of a long period during which living things existed without fossilization is a reasonable one. Some biologists, however, even at the present time have not been greatly impressed with the reasons for expecting a long period of antecedent evolution before fossils were readily formed, have regarded Cambrian diversity as having actually arisen as suddenly as it appears to have done, and have drawn some curious conclusions as to the rate of early as compared with subsequent evolution. Entirely apart from the doubt which these few biologists entertain regarding the history of Pre-

Cambrian life, no emphasis is here placed on the probability of an abundance of organisms in Proterozoic and earlier periods. For the purpose of this chapter is not to explain the discrepancies of geological history, by making evolutionary assumptions; it is rather to discover to what evolutionary conclusions one is driven by consideration of the patent facts regarding fossils. Viewed in this light, Cambrian does present the outburst of life that is so apparent. It is from that period that the paleontological story of evolution must start. Let us see what the beginning was.

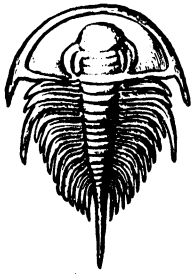


FIG. 9.—A trilobite.*



FIG. 10.—A brachiopod.*

The most abundant of all fossil forms in the Cambrian were the trilobites, which belong to the Crustacea, and were more nearly like modern fairy shrimps than any other living group. They have long been extinct. The body was flattened, and marked by longitudinal grooves into three lobes (Fig. 9), hence the name. The trilobites increased throughout Cambrian time, both in numbers of individuals and numbers of species; over 300 species have been described from that period. Next in abundance were the brachiopods. These animals superficially resemble clams, because they possess a shell of two hinged valves (Fig. 10). They were long classified with the mollusks, until it was appreciated that their internal structure was not at all that of mollusks, and that the two valves, instead of being right and left as in clams, were dorsal and ventral. The Cambrian brachiopods possessed shells mainly of a horny substance. Hundreds of species are known from Cambrian marine deposits.

Mollusks were less abundant than either of the foregoing groups but were represented by each of the principal classes—

* From Pirsson and Schuchert's Textbook of Geology. John Wiley & Sons. By permission.

the clams, the snails (mostly not spiral), the pteropods and the cephalopods. Of the echinoderms, there were a few starfishes and a few sea cucumbers, and a somewhat larger number of the primitive and extinct group known as cystoids. The worms, soft-bodied as they are, were not often preserved as fossils. A notable exception is the Burgess shale, in which a great variety of impressions of worm bodies are preserved. Elsewhere their presence in the Cambrian is abundantly indicated by their tracks and burrows in the mud. Jellyfishes are even less likely to be fossilized than are the worms, yet in many places in both America and Europe are found casts of the interior cavities of their bodies. Other coelenterates, including corals and the extinct hydroidlike graptolites, the former abundant enough to constitute reefs, have been assigned to the Cambrian, though there is some doubt regarding both the affinity of the organisms and the identification of the containing rocks. The sponges, as might be surmised, are identifiable only by the needlelike spicules of their skeletons, but these are fairly common. Protozoa, the one-celled animals, were represented by both Foraminifera and Radiolaria.

The animals mentioned above belong to at least eight of the main groups or phyla. The worms probably all belonged to the Annelida, though it is possible that one of the other wormlike phyla was included. Assuming, however, that the other worms are not included, there remain only two other phyla of minor importance, and one major phylum, chiefly the vertebrate animals, unaccounted for. Since all of these omitted groups with the exception of the vertebrates were soft-bodied, they may easily have existed in Cambrian time. Even the vertebrates may not have been absent, since fishes appear in the very next period, and an object that looks like one of their scales has been found in Cambrian rocks. It is thus clear that in Cambrian time most of the great groups of animals were already in existence.

Of plants, only fossil sea weeds have been found. Land plants are unknown, though if the vascular plant from Czechoslovakia mentioned on page 46 proves to be really Algonkian it would be almost necessary to suppose that such forms continued through Cambrian, since they are found in periods not much later. Abundant plant life in the sea may be inferred on the ground that the animals must have been ultimately dependent, as they are now, upon plants for food.

The further history of life on the earth can best be told in relation to the several groups of organisms, rather than to the geological periods.

The Arthropods.—The trilobites, with which the arthropods began so auspiciously in the Cambrian, waxed more abundant in the Ordovician, but reached their peak in that period with nearly a thousand known species belonging to 77 genera. Only seven of these genera, however, are the same as those of the preceding Cambrian. Of the 13 families to which these 77 genera belonged, only three survived from the Cambrian; the rest were new. No new family arose after the Ordovician period, though new genera continued to appear. Only about half as many species of trilobites have been found in Silurian deposits as in Ordovician, and none of these is a survivor from the Cambrian. The group was obviously declining, a change that continued through the Devonian. New species and new genera appeared during this decline, but larger numbers of both species and genera became extinct. The decline was accompanied by curious ornamentation of the head and the development of remarkable spines on the head and tail in the new species that arose. Trilobites were rare in the Carboniferous period, and none whatever has been known since Permian.

The eurypterids, resembling scorpions but living in the sea instead of on land, appeared first in upper Cambrian, were still unimportant in Ordovician, increased in numbers and size in Silurian, and reached their maximum in both size (10-foot specimens being found) and variety in Devonian. Thereafter they declined, and the last ones known came from Permian deposits.

The horseshoe crabs, which first occur in the Silurian of Europe, never attained great variety or abundance, but they have survived to the present time. During the earlier geological periods, different genera arose successively, but by Jurassic time only the genus Limulus existed, and this genus survives today on the east coast of the United States and in the Molucca Islands. Probably only so old a genus could now occupy two such widely separated areas.

The earliest known insects are from the Pennsylvanian division of the Carboniferous, though their great abundance and size suggest that they had existed much earlier. Over 800 species

of cockroaches have been described from the Pennsylvanian, and it has been proposed that that period be called the "age of cockroaches," though from the standpoint of numbers of individuals dwellers in urban centers of the present time would probably challenge the right of any geological period to that phrase as a distinctive name. The average size was about 2 inches in length; some cockroaches were 3 or 4 inches, other insects 12 in., and some resembling dragonflies had a wing spread of more than 2 feet. Never since Pennsylvanian and early Permian have insects been so large, and it is suggested that the decline in size was correlated with the onset of colder climates. In Permian time the dragonflies and May flies were the most conspicuous. Late in that period appeared the first beetles, in Australia. In Triassic, for some unknown reason, insects were scarce, only about 30 species of all kinds being known; but they blossomed forth again in the Jurassic with multitudes of individuals and such new types as grasshoppers, bees, wasps, ants, flies and butterflies. Almost all insects of Jurassic time were smaller than in the preceding ages and were of quite modern type. No very important change in them is revealed during the Cenozoic era, though fossil insects of that time are not very numerous. Insects are today probably more abundant in species than any other group, and more abundant in individuals than most others.

While arthropods of other kinds have been found, they were not very favorable for fossilization, and connected accounts of their changes are not so readily available.

The Brachiopods.—At their beginning in the Lower Cambrian, the brachiopods were mostly of a group having horny shells, but later in that same period they were chiefly of calcareous type. The latter became increasingly prevalent in later periods. Brachiopods increased greatly in Ordovician, their increase being accompanied by the appearance of new species and new genera, and the loss of old ones. Two of the families gained at the expense of all others as the group went over into the Devonian, and in this period the group attained its greatest abundance and diversity. During the Carboniferous period brachiopods maintained their individual abundance, but a decline set in in the number of species and genera. New kinds were coming into existence, but they were more than offset by

the loss of older forms. This decline continued, though slowly, so that throughout Paleozoic time brachiopods were so abundant that they are extensively used by paleontologists as index fossils. Being of different species and genera in successive ages, and being of well-nigh world-wide distribution, they have been used to correlate deposits in widely separated areas. Their value for this purpose was greatly diminished in Mesozoic time because, while they were fairly abundant in Europe, only a few genera were left by Jurassic time and North America, for some unknown reason, was poor in them. Through the Cenozoic era they were inconspicuous, but about 160 species have survived to the present.

The decline of the brachiopods is notable for the tenacity with which certain genera maintained themselves. The very considerable diminution in number of species and genera which began in the Carboniferous involved the destruction of most of the genera of Devonian time; yet among the survivors were several genera that first appeared as early as Silurian. Even more striking examples are the genera Lingula and Crania, which were among the earliest of the Cambrian forms, and were of the horny-shelled type that was largely displaced by the calcareous type before the end of Cambrian, but which are still in existence, living, at the present time. These brachiopods thus exhibit even greater permanence (stability, it would be called, with the evolution concept in mind) than the Limulus mentioned above among the arthropods. No satisfactory explanation of the persistence of a few genera, when nearly all genera are much more short-lived, has ever been offered.

Bivalves and Snails.—As stated above, the mollusks were already divided into their main classes when they were first preserved in the Cambrian. All of these classes increased greatly in the Ordovician. For the clams, this increase was largely one of numbers; for the snails it was a change in numbers and kinds, and in size, particularly among the spiral-shelled forms. In both of these classes there was moderate further increase in variety through the remainder of the Paleozoic, and their numbers were well maintained. Clams and snails are not, however, particularly good index fossils for the Paleozoic era, because their distribution was at times limited. In some situations they were abundant, elsewhere lacking. This may be in

part due to the rather ready solubility of the mother-of-pearl which lines their shells. This layer was relatively thick in the early mollusks. The outer material, which is less soluble, was relatively thicker in the later forms, and this feature may have helped to preserve them. At any rate, in the Mesozoic both clams and snails were much better represented, and were far more varied, than in the preceding era. One striking development among the snails was the first occurrence, in the Triassic, of shells whose lip was drawn out into a grooved siphon; shells of this type became abundant in the Jurassic. Oysters (bivalves) first became abundant enough to form banks in the sea in Jurassic, such banks being duplicated in the Cretaceous. By the end of the latter period bivalves were largely of modern type, many of the genera then existing being still living at present. Snails reached their general modern composition by the end of Cretaceous, owing to the appearance then of genera which have persisted throughout Tertiary time to the present. Although oysters attained in the Miocene a size which they possessed neither before nor after that time (fossils from California measuring 13 by 8 by 6 inches), these two groups of mollusks can not be said to have culminated in any past period; for, with their more than 40,000 species, they are as abundant and as diverse now as they ever have been.

The Cephalopoda.—Owing to the very different history of the cephalopods, as compared with the bivalves and snails, it was not possible to render a single account of the changes experienced by the whole group of mollusks. Whereas bivalves and snails have continuously increased in importance from Cambrian to the present, with relatively slow progress during the Paleozoic, the tetrabranchiate (four-gilled) cephalopods staged a whirlwind rise, followed by a slow decline and almost total extinction. Already in the Ordovician the cephalopods were one of the chief groups of marine forms. The commonest cephalopods of Ordovician possessed straight conical shells, divided by partitions from the apex of the cone to a level near the base, but leaving at the base an undivided space in which the animal lived. There were some with wide bulging shells, others with curved or coiled or partly coiled shells, but the straight cones were predominant. These latter, which are called orthocones, persisted a long time, but became less and less abundant during each geological period

until their extinction in the Triassic. In the Silurian the orthocones were somewhat less numerous and were commonly ornamented with ridges, while the bulging ones (which in addition had a restricted T-shaped opening next the animal) were more abundant than before. Yet the characteristic cephalopods of this period were those with coiled shells. With the Devonian there was ushered in a change in the shape of the partitions across the shell. Heretofore they had been flat saucer-shaped plates whose edges joined the shell in a relatively straight line. In the Devonian there appeared cephalopods in which the edges of the partitions were bent at several places into sharp angles separated by high saddlelike curves. A further change came in the Carboniferous when, among the many new genera, there were some with the partitions bent into many shorter U-shaped curves marked at characteristic points by a zig-zag or saw-toothed course, and some with partitions exhibiting patterns like lobed leaves. The latter type became more abundant in the Permian, the pattern of their partitions reached their greatest complexity in Triassic, the greatest number of species of this kind occurred in Jurassic, and they died out in Cretaceous. With them perished all remaining tetrabranchiate cephalopods except the coiled forms having simple partitions, which are known as nautiloids. The nautiloids exist at the present time in a very few deep-sea species.

Along with the change in the general form of the shell and of the partitions, there were developed at different times numerous nodules and ridges on the shell. Also, toward the end of their cycle, the coiling of the shells underwent various changes. Shells that are tightly coiled at the center and loosely coiled in the outer rings, or tightly coiled at the small end and straight in the larger portion, forms which are now generally regarded as degenerate, were quite common in the Cretaceous.

There was another group of cephalopods, the dibranchiate (two-gilled) type, which first appeared in Triassic and exists at present, including the squids and cuttlefishes, but their history was much less striking. The belemnites, which belong to this group, were of great variety in Jurassic, and were still abundant in Cretaceous, but disappeared soon thereafter. No later member of the dibranchiate group occupied an important place in the animal life of its period, and such forms are of minor

significance today. The spectacular role of the cephalopods was thus played entirely by the tetrabranchiates. These latter forms were so abundant, so varied, and so characteristic of the respective strata that they have been universally used as guide fossils of the Mesozoic era.

The Echinoderms.—Most of the Cambrian members of this phylum were of the now extinct class of cystoids, though there were some starfishes and sea cucumbers. Of this whole phylum, only the crinoids and sea urchins appear abundantly enough to furnish a real history of their changes. The crinoids were present but not common in Ordovician, increased in numbers and variety through the succeeding periods, and reached their maximum (about 600 known species in North America) in the Mississippian. They were reduced in numbers but began to be radically changed in structure to conform to the modern type in Jurassic, after which the new type became in turn abundant. Free-swimming species first appeared in Jurassic, and were locally abundant. Since that time they have been relatively unimportant. The sea urchins, which appeared rarely in Ordivician, did not become abundant until Jurassic and Cretaceous. They are today the commonest of echinoderms. Two striking changes in their structure are demonstrated by the fossils. First, modern sea urchins have 20 rows of plates in their tests, or shells, while all Paleozoic members of the group have either more or fewer rows. Second, forms showing right- and left-sidedness appeared first in Jurassic; all earlier species had been radial.

The cystoids, which were the chief echinoderms of Cambrian time, reached their greatest diversity and abundance in the very next period, then began to decline, though new genera appeared from time to time, and were extinct by the beginning of the Carboniferous.

Other Invertebrates.—Of the remaining invertebrate phyla, the ones most commonly met with in marine deposits are the coelenterates, sponges, and protozoa. Whether any of the corals, or the graptolites which resemble somewhat the modern hydroids, were present in the Cambrian is still debated; but in the Burgess shale, where some of the most remarkable preservations of ancient life occur, there are unmistakable impressions of jellyfishes. The graptolites reached their maximum in the Ordovician, in forms arranged in rows on both sides of the stem. By

Silurian time they were much reduced, and were mostly those forms with only one row of individuals; and before the end of the Devonian they were extinct. Corals of both the hydroid and the true (anthozoan) type were present in Ordovician, the former abundant enough to produce reefs. The true corals of this time possessed partitions in multiples of four, as contrasted with six in modern corals, a type which did not make its appearance until the Permian. Both types of corals (hydroid and anthozoan) expanded rapidly, in species rather than in genera, from Ordovician to Devonian, but suffered reverses in the Carboniferous and Permian, since reefs were reduced in the former, and wanting in the latter of these periods. In later periods they regained their abundance, but the true corals were then of the basic six-partition type as are the reef builders of the present.

Sponges are preserved only with respect to their skeletons of spicules, and these show characteristic changes of form. The protozoa are represented only by shelled forms, mostly Foraminifera and Radiolaria, which constituted so small a part of the probable protozoan life of any period as to make the history of their changes unimportant for our present purpose.

Land Plants.—Sea weeds, which do not fossilize easily, are known from Cambrian and Ordovician. It is not to be expected that plants would be well preserved until they possessed woody structures. Unless the one vascular plant already mentioned is correctly assigned to the Algonkian, there is no very good evidence of these woody land plants until the Devonian. Fragments resembling the Devonian species have been sparsely reported from Silurian, but these may be ignored. The early Devonian land plants were mostly devoid of leaves, or their leaves were mere scales. One important group of that period, the pteridosperms, was long regarded as belonging to the ferns, but it is now known that they bore seeds, which modern ferns do not. Stems of some of these were three feet in diameter. The lycopods, or club mosses, whose modern examples are such small plants as the ground "pine" and the creeping Selaginella, were then trees, up to 30 feet in height. Trees resembling the pines, firs and spruces also existed then, but they did not possess needlelike leaves.

The giant treelike club mosses (Fig. 11) were very abundant in the Carboniferous, and grew in all the northern continents;

but by Permian time they were rare, and were missing from the Triassic. Other less conspicuous members of the lycopods were present, however, and they constitute an unimportant group now.

The horse tails of the upper Carboniferous were trees with transverse joints, some with branches, some without. They were still abundant and large, though largely of different genera in Triassic and Jurassic. Since then they have gradually taken on the characteristics of the modern members of the group, the scouring rushes, which are reduced to one genus and some 25 species, very few of which grow over several feet in height.

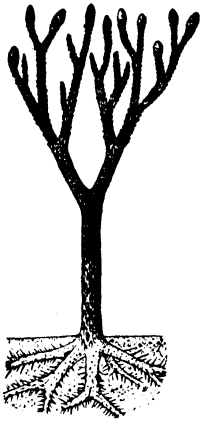


FIG. 11.—Giant club moss from the Pennsylvanian.*

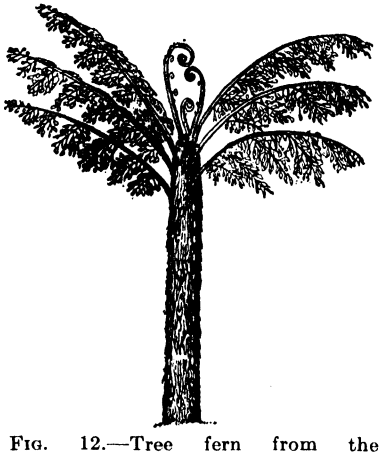


FIG. 12.—Tree fern from the Pennsylvanian.*

The pteridosperms, referred to above in the Devonian as having been regarded as ferns until they were found to be seed bearers, reached their maximum development in the Pennsylvanian. They were still abundant in Permian, much less so in Triassic, and after that disappeared. The separation of the pteridosperms into a distinct group has left the early ferns much diminished. The ferns (Fig. 12) were common, however, all through late Paleozoic, uncommon in Triassic, but abundant again from Jurassic to Eocene. After that they were mostly replaced by modern plants, though there are still many ferns today.

* From Pirsson and Schuchert's Textbook of Geology. John Wiley & Sons. By permission.

The Devonian "conifers" had straplike leaves, rather than needle-shaped. The same kinds of leaves are found on those of the Mississippian and Pennsylvanian (Fig. 13). They are classed with the conifers, though their seeds, instead of being borne in cones, were situated on small budlike branches. Cones first appeared in late Pennsylvanian and early Permian, on a tree that had narrow leaves. The splendid petrified trees of the far southwestern states were conifers of Triassic time; some of them show annual growth rings, indicating seasonal differences of climate, though perhaps not temperature extremes. Conifers remained abundant through Jurassic, though then overshadowed by cycads, and in late Cretaceous they were almost suddenly submerged by a great invasion of true flowering plants.



FIG. 13. Large-leaved Pennsylvanian evergreen, Cordaites. (*From Pirsson and Schuchert's Textbook of Geology. John Wiley & Sons. By permission.*)

The cycads began in the Pennsylvanian, in what may almost be regarded as modified pteridosperms. A few true cycads occur in early Triassic, many more in late Triassic, mainly represented by their leaves. In Jurassic they became so abundant that this period is often known as the "age of cycads." In late Cretaceous, however, they were largely overwhelmed by the flowering plants, and today they constitute an unimportant group of which the sago "palm" is the most familiar example. Somewhat similar to the cycads are the ginkgos. Appearing first in Permian time, they became abundant in Triassic and expecially Jurassic. With the coming of the flowering plants in upper Cretaceous, the ginkgos too receded in importance, and the group is today represented by only one species, widely cultivated as an ornamental plant and probably nowhere wild.

The true flowering plants appeared suddenly in such abundance and variety in late Cretaceous that it is generally assumed they originated much earlier, though little fossil evidence of them in earlier periods has been obtained. One genus of plants in upper

Triassic had its seeds enclosed in a berrylike fruit, and two genera in Jurassic time also have the seeds so contained. Since a fruit, containing the seeds, is one of the special characteristics of the flowering plants, as contrasted with the naked seeds of conifers and ginkgos, it is possible that these several early plants are to be allocated to the former group. In late Cretaceous flowering plants are so abundant and appear so abruptly that it is generally believed they must have migrated into the places where they are found, from other regions in which they either were not preserved or which have not been explored, possibly from arctic areas. It

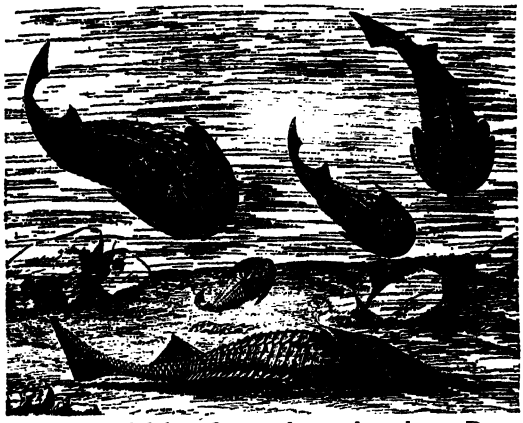


FIG. 14.—Small armored fishes, Ostracoderms, from lower Devonian. (*From Pirsson and Schuchert's Textbook of Geology. John Wiley & Sons. By permission.*)

is the woody or otherwise hard plants that are preserved, and the late Cretaceous forests include oaks, beeches, maples, elms, poplars, magnolias, tulip trees and palms, and grasses are also abundant in the open places. The forests were thus very much like those of the present. The changes that have occurred since then are largely concerned with distribution, as in the Eocene trees of Greenland which were like those now in the Atlantic states in the latitude of Virginia, and the Miocene plants of Europe which were similar to the flora of modern India.

Fishes.—Unless an object that looks like a scale of a primitive fish, found in Cambrian, is really such, the earliest known vertebrates are Ordovician fishes of the group known as Ostracoderms, found in Colorado, Wyoming and South Dakota. The deposits in which these fossils are found are interpreted as having been

laid down in fresh water. These armored fishes (Fig. 14), mostly of small size, reached their maximum abundance in Devonian, and perished in that period. The lampreys appeared in Silurian time, as did also the sharks, and lungfishes followed in Devonian. So abundant and varied were these groups that Devonian is called the "age of fishes." The extinct armored Arthrodira, some of them huge animals (25 feet long), and the ganoid fishes, whose few modern survivors include the gar pikes, were also then prominent. There were, however, no true bony fishes (teleosts) in Devonian, the first of these occurring in Jurassic. The several groups fluctuated in their abundance: sharks were dominant in Mississippian, but declined thereafter; ganoids were at their peak in Jurassic. Changes also took place in their structure, one important instance being the almost complete substitution, by Jurassic time, of sharp-pointed teeth in sharks for the flat-topped ones presumably used for crushing shells. The ganoids almost disappeared by Cretaceous time, their place being taken by multitudes of teleosts, or bony fishes, and these, by early Tertiary, exhibited most of the families that exist today.

Amphibia.—The history of the amphibia is so incomplete that the chief reason for including them here is to indicate the extreme difference between the only fossil group that is known to have been abundant and the modern types. A single footprint in upper Devonian sandstone in western Pennsylvania is the earliest indication of this class. Numerous amphibian tracks occur in the Tennessean. They are identified by comparison with tracks and the fossilized salamanderlike animals in Pennsylvanian and Permian time, when at least 20 genera of amphibia lived. These animals were mostly of the group called Stegocephalia, or similar to them. They possessed a tail, an armored head and belly, and short legs or none at all, and varied in size from a few inches to 8 feet in length. They became extinct in Triassic. Real salamanders, unarmored, date from the Comanchian, and have been found occasionally in Oligocene, Miocene and Pliocene.

The oldest known frogs lived in the Jurassic of Spain and Wyoming. Others, belonging to living families, have come from the Oligocene of Europe and Mongolia and the Miocene and Pleistocene of Europe. The only known fossil tree frog is from the Miocene.

Reptiles.—The earliest known reptiles are found in upper Pennsylvanian deposits. They increased remarkably in Permian, as not only new species and new genera appear, but new families and orders. Most of them looked like large lizards, some of them with a large finlike projection upon the back. Even more extraordinary was the array of reptiles in the Mesozoic, which has been termed the "age of reptiles." It is the dinosaurs which are the conspicuous members of the group, owing to the huge size which some of them attained. Not all were large, however; they

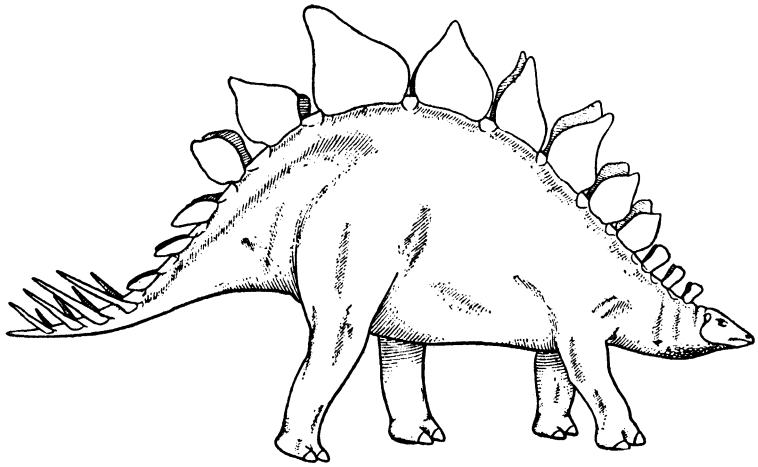


FIG. 15.—Comanchian dinosaur, Stegosaurus, with 10-ton body and 3-ounce brain. (*From Pirsson and Schuchert's Textbook of Geology. John Wiley & Sons. By permission.*)

ranged from the size of a hen to 150 feet in length. The huge bodies bore ridiculously small heads. Some dinosaurs were vegetable-feeders, and these were often horned; they are found only in the Cretaceous. Others were carnivorous, and these were usually hornless. The dinosaurs as a group appeared first in middle Triassic, a little earlier in America than in Europe. By Jurassic or Comanchian—there is some doubt about the date of certain deposits rich in dinosaurs—they had become very numerous and varied. Armor plates curved over the head and neck, spines, plates set on edge along the back or along the sides (Fig. 15), were common extravagances of structure. Some walked only on their hind legs, the forelimbs being greatly reduced. Mummified skins and dried carcasses show them to

have been covered with scales as are modern reptiles. That they laid eggs is shown by fossil eggs discovered in Mongolia. Before Cretaceous many of the large dinosaurs had died out, and very few of the group—none in North America—survived to the Eocene. New groups kept appearing, while the order lasted, for the spoon-billed dinosaurs began and ended in the Cretaceous.

Other curious reptiles of the Mesozoic were the ichthyosaurs, or fish-lizards, of the Jurassic and Comanchian; plesiosaurs, marine predaceous swimmers of Jurassic to Cretaceous; and pterosaurs, the flying reptiles, whose wings consisted of skin stretched between the body of the hand and a greatly elongated fifth finger.

The earliest known turtles and tortoises lived in Triassic time, true lizards first appeared in Jurassic, and the first snakes are found in the Cretaceous. These are the groups that have survived most plentifully to the present time. Tortoises were abundant in Eocene and huge in Miocene, and lizards increased considerably in Oligocene. Venomous snakes did not arise until mid-Tertiary.

Birds.—The earliest fossil birds are of upper Jurassic. Two skeletons belonging to different genera, named Archaeopteryx (Fig. 16) and Archaeornis, and a feather of a different species, constitute the entire find of that period. The beaks of these birds were not horny, and the jaws bore small teeth, unlike modern birds in both respects. The tail was much longer than in living birds, and quill feathers were borne in pairs on opposite sides of it. The bones of the hand were very much better developed than in modern birds, and each finger ended in a claw. The few birds of the Cretaceous—Ichthyornis and Hesperornis—had lost some of their anterior teeth of the upper jaw, and a horny bill was partially developed. The former was a small bird with well-developed wings, while the latter was 6 feet high and had very small wings presumably useless for flight.

By Eocene time most of the present orders of birds were in existence. The vultures, owls, quails, gulls, ibises, pelicans, eagles and woodcocks of that period differed little from the corresponding birds of today. There were, however, some large flightless birds in Wyoming unlike any now living. Later periods preserved few birds, particularly in America. In France some heaps of Miocene bird bones have proved to be of African types,

and include parrots, secretary birds, adjutants, cranes, flamingoes, Indian swallows, land grouse and pelicans, intermingled with some owls, woodpeckers, eagles and ducks of European appearance. The fossil history of birds is thus very meager.

Mammals.—Small mammals, the first of this group, have been found in Triassic deposits of Germany, mostly as separate jaws whose teeth show they were not reptilian. The group was still poorly represented in Jurassic, again mostly by jaws, though



FIG. 16.—Archaeopteryx, fossil bird of upper Jurassic. (*Courtesy of American Museum of Natural History.*)

South Africa has yielded most of one skull and one of the leg bones. Enough variety exists among these fragments to allocate them to four different orders, all of which are now extinct. Even in Cretaceous relatively few mammals have been found. America and Mongolia have provided some, but Europe none at all of that period. All are small, but there is little to indicate their characteristics.

With the Eocene there began a rapid rise of the mammals, in numbers, size, diversity, and occasionally sheer oddity, which is unparalleled in any other group save the reptiles of Mesozoic time. While some of the archaic types of the preceding periods lived over into the Eocene, or even the Oligocene, the great

development was the beginning of most of the modern groups. Here were the little four- and three-toed horse; the earliest ancestors of camels and pigs; the rodents, which are now the most abundant of all orders of mammals; the first carnivores; the beginnings of tapirs and rhinoceroses; the first sign of elephant characters; the titanotheres, long since extinct; and the primitive monkeys. The rapidity with which all this change occurred suggests immigration from some region not yet explored, perhaps Asia. One curious group deserves mention as showing how quickly bizarre forms may appear in a class of animals. This was the Dinocerata. One member of this group was as large as an

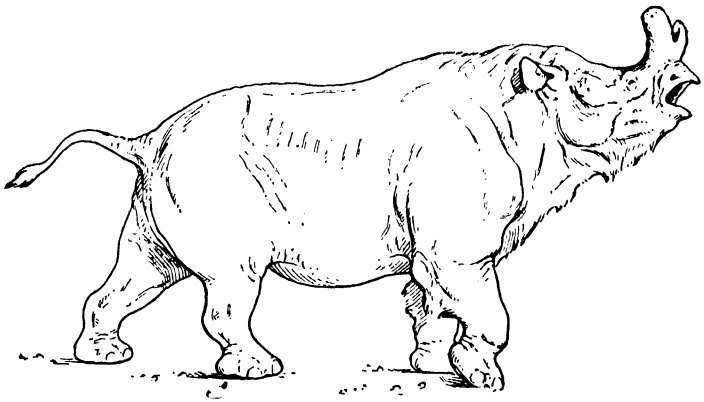


FIG. 17.—A titanothere, Brontotherium. (*From Pirsson and Schuchert's Textbook of Geology. John Wiley & Sons. By permission.*)

Indian elephant, had sharp-edged tusks in the upper jaw, and bore six large bony protuberances on the top of its head. This entire group existed, so far as fossils show, only in Eocene.

Only a few of the later developments can be given here. True carnivores existed in three families, the wolves, weasels and cats, in Oligocene time. Saber-toothed cats appeared first in the Oligocene, the true cats not until Miocene. Horses became larger, their lateral toes became reduced, and their skulls and teeth changed considerably over a large part of the Tertiary. Camels underwent a somewhat parallel change in size, feet and teeth. The titanotheres, huge animals with little brains and a pair of bony pegs on the nose (Fig. 17), died out in the Oligocene. Mastodons, the primitive browsing elephants, occurred in Miocene, apparently first in Africa whence they spread into all the

northern continents, and lived until early human historic times. They were followed by the flat-toothed grass-eating elephants. Grazers arose also in other groups of mammals in the Oligocene and became much more abundant in Miocene, as in the horses, rhinoceroses, camels, the ruminants, many rodents and some pigs. From the grazing teeth of these animals it is inferred that grasses were abundant on the plains. The whales and dolphins appeared first in Miocene. A curious burrowing mammal, Epigaulus, with two conical horns on the top of its head, lived in Miocene and Pliocene. During these later periods there were many mammals belonging to well-defined groups living at present, including not a few modern genera.

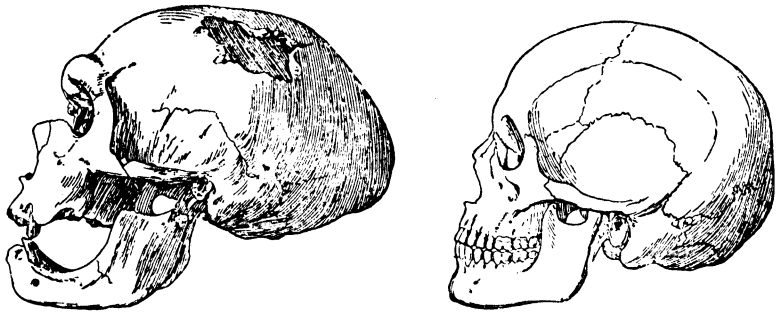


FIG. 18.—Neanderthal skull (left) beside modern human skull. (*From Pirsson and Schuchert's Textbook of Geology. John Wiley & Sons. By permission.*)

The primates have never been well represented as fossils. As indicated above, there were primitive monkeys in the North American Eocene, but not a single member of this group has been found in any later period in this continent. The earliest known South American monkeys were of the Miocene, and rare. Monkeys and apes occur sparsely in the European Pliocene, and monkeys in the South American Pleistocene. In each period in which South American monkeys have been found, they were of the groups still characteristic of South America as distinguished from the rest of the world. Fossil men or manlike apes have been discovered in fragments at different levels of the Pleistocene and at various places in Europe, Asia, Africa and the Malay Islands. The principal ones of these may be mentioned briefly. *Pithecanthropus erectus*, of the Pleistocene in Java, known from a skull cap, several thigh bones and three

teeth, was nearly erect (judging from the nearly straight form of the femur) and about 5½ feet tall. Its brain capacity, according to recent studies, was about 900 cc., or nearly as great as modern savage men. Heidelberg man, also of Pleistocene, is represented only by a lower jaw, whose chinlessness is apelike but its teeth nearly human. Piltdown man, *Eoanthropus dawsoni*, whose jaw was like that of a chimpanzee but the skull human, is referred to middle Pleistocene. Neanderthal man (Fig. 18), the first to be known from nearly complete skeletons, was distinctly a man, with large brain capacity, a stooping posture, an apelike face, and 5-foot stature. He lived in late Pleistocene time. He was supplanted in Europe by the 6-foot, large-brained, immigrant Cro-Magnons whose tools and works of art marked them as mentally far superior to any that preceded them.

Mammals in general suffered a great destruction following the Pleistocene. At few points in geological history has there been extermination comparable with that of mammals in time just preceding the recent. In part this may be due to repeated glaciation, but most of it is unexplained. Only the tropical regions, notably Africa, escaped this great diminution of mammals, and the Pleistocene mammals of that continent were essentially the same as today.

Evolutionary Implications of Fossils.—It is clear from the very much abbreviated account in this chapter that the animals and plants living on the earth at one time differed markedly from those of other ages. If it be assumed that there is a genetic continuity among these forms, or among any considerable portion of them, there can be no denial that evolution has occurred. If the animals of today have descended from the animals whose fossils are found in Tertiary or Mesozoic or earlier deposits, or if both modern and fossil types have sprung from common ancestors which were never fossilized, there is implied a considerable amount of change accompanying descent. Biologists have assumed this genetic continuity because the alternative explanations have seemed incredible or impossible.

One of the alternatives long ago suggested was that life had been repeatedly destroyed and then recreated of a different type. The great Cuvier expounded and defended this theory of catastrophism. It was more credible in his day than later. Rela-

tively few fossils were then known, and his attention was no doubt strongly drawn to the very great transformations of the living world which occurred between the major eras. It is notable that at the end of Paleozoic, and at the end of the Mesozoic, or between each of these eras and the one following, there was a very striking change in the general nature of the animals. It is these differences that serve to indicate the limits of the major divisions of geological time. If one looked principally at the animals and plants on opposite sides of one of these dividing planes, and especially if the representatives of both groups were not too numerous, it would be easy to get the impression that life was destroyed and recreated in new guise. When, however, it is observed that similar though less marked differences are found at every level within each era, the small number of catastrophes which might have satisfied Cuvier no longer suffice. Destruction must occur in one group while others are thriving remarkably, or even while others are being created. If catastrophism is the correct explanation, the catastrophes must have been in the main small ones affecting only a single group at a time. This conception of frequently repeated creations is not very different from evolution in its general consequences, and this particular alternative to evolution has not been seriously supported by any responsible person in recent years.

The suggestion is still occasionally made that fossils and living things are simply different types, all of which have been in existence since the beginning of life, and some of which have become extinct. This explanation overlooks the fact that living species are seldom found as fossils. Present-day genera often go back several geological periods, a few much farther. There is no reason why an animal whose descendants subsequently became extinct should have been preserved any more readily than one whose descendants lived to the present. Yet, if all species have been in existence from the beginning, that is precisely what must have happened to account for the absence of present species as fossils in ancient rocks. Even after taking into account the imperfection of the geological record, it must be concluded that modern animals are seldom or not at all represented by fossils because they were not in existence in those earlier periods.

In this chapter no stress is laid on the regions of the earth in which the fossils have been found. Many differences between the fossils of South America and the northern continents, and between Australia and the rest of the world, could have been pointed out. The significance of these contrasts is essentially similar to that of the distribution of modern animals, described in the preceding chapter. The general conclusion there drawn regarding the origin of species is reinforced by the facts from fossil animals and plants, namely, that species have arisen at widely different times and places. Evolution as the mode of origin of species harmonizes admirably with this conclusion; other possible modes of origin have to be strained to produce any approach to agreement with the facts.

CHAPTER V

THE MATERIAL BASIS OF EVOLUTION

> The germ cells are the only living bonds not only between generations but also between species, and they contain the physical basis not only of heredity but also of evolution.
>
> E. G. CONKLIN, 1934.

Assuming that considerations of the sort outlined in the preceding chapters are sufficient to indicate that a process of evolution must have occurred, we may now inquire how such changes may have been brought about. The remainder of this book is an attempt to answer this inquiry. While the details of the process are the subject of much speculation, and much difference of opinion exists even in some major departments of the theory, there is ample ground for unanimity regarding a few fundamental concepts. In the last-named fortunate state is the general idea of the physical substratum in which evolutionary modification must be sought.

The clue to the seat of evolutionary changes is furnished by the remarkable degree of obstinacy of species. Notwithstanding considerable changes in their environment, partly diurnal, partly annual, partly secular, partly capricious, they maintain their characteristics over long periods of time with striking precision. Compared with their stability, the evolution of species is slight. Though the present condition of a species is the result of the modification of a previous somewhat different constitution, the changes are preserved with great tenacity—always subject to modification, but experiencing it infrequently. The biologist's name for this persistence of the qualities of organisms is heredity. The easiest way to bring about modification of a species, with a high degree of stability of each new state, would be to introduce the changes into the hereditary units; and there seems to be little doubt that that is actually what has happened. The physical basis of evolution is thus identical with the physical basis of heredity.

The Genes.—Most of the phenomena of heredity are traceable to the genes. These are minute bodies located in the nuclei of the cells of the organism. They are in and form a part, though certainly not all, of the deeply staining substance known as chromatin. These genes are in a sense independent units, in that they are capable of behaving in different ways, but there are many restrictions put upon their movements by the remaining parts of the genetic mechanism. They are the governors of the organism's activities. Each gene has a different effect from every other gene, but none of them ever does anything by itself. Usually each gene has a more easily observable and probably larger effect on some one part of an organism, say the color of the eye, than it has on any other part. Hence it is commonly called the gene for this or that character, as the gene for eye color. It should not be forgotten, however, that there is always more than one gene affecting a visible character, and that every gene has more than one effect. These features of the genetic mechanism will be made clearer in a later chapter.

The above facts about the actions of genes will at once suggest that there must be a multitude of them. If several of them are necessary to fix so small a feature as the eye color of an animal, it would seem that a very large number would be required to determine a whole organism. Just how many genes there are is not known for any living thing; but for the animal whose heredity is best understood, the vinegar fly Drosophila, there are several ways of making an estimate. Most of these estimates fix the number at 3000 to 5000, though one of them is about 28,000. It may be conjectured that simple organisms have fewer, complex organisms more, than Drosophila has.

Whether individual genes can be separately seen is questionable. At certain stages of the cyclical changes of cells, there may be seen in their nuclei numerous minute bodies showing the arrangements which experiments show genes to exhibit, and some geneticists and cytologists regard these dots as the genes. In one of the most favorable objects of study (the lily) about 2200 of these small objects can be counted in a single cell (Fig. 19). This is near enough to the number estimated for the vinegar fly to lend some color to the belief that they really are the genes. In most organisms, however, the number of visible bodies is much smaller, and it seems likely that the objects seen are often

if not always collections of genes. And even when there is but one gene in each dot, it is quite likely that the gene is not the whole visible object, but that other inert material accompanies the active gene.

The nature of the genes is conjectural. There are important reasons for regarding them as protein bodies. They occur in nuclei which, by special treatment, have been separated from their cells in quantities sufficient to make chemical tests, and have given protein reactions. They possess a high degree of

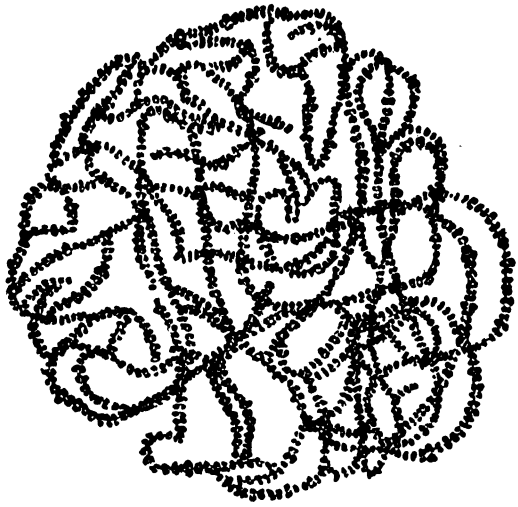


FIG. 19.—Minute nodules of chromatin, called chromomeres and regarded by some as the genes, in a lily cell. (*From Belling, Univ. Calif. Publ. Bot.* 14.)

specificity, that is, the capacity to do certain things and only those things; and such specificity is a recognized characteristic of protein substances in general. Add to these considerations the fact that one of the principal chemical differences between living and nonliving matter is the prevalence of proteins in the former, and the conclusion that the most fundamental of all living constituents, the genes, are of protein composition attracts strong support.

Chromosomes.—The genes in a cell are not jumbled together in orderless fashion; they are on the contrary joined together in strings in a very regular scheme. Each string of genes, with whatever inert chromatin accompanies them, constitutes a

chromosome (Fig. 20). Now, the genes are mostly different from one another. They are usually alike by pairs, or sometimes even by quadruplets, or as a result of some abnormality by triplets. The scheme of twins is the ordinary one, so that an organism having 5000 genes has 2500 different kinds of genes.[1] Each chromosome is regularly made up of certain of these different kinds of genes, which are arranged in a definite order from one end of the string to the other. The chromosomes thus possess

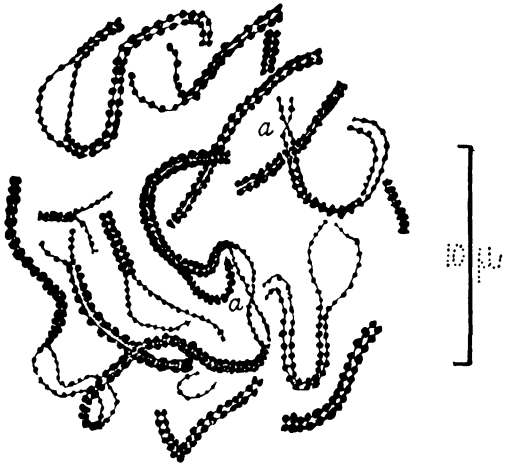


FIG. 20.—Strings of chromomeres (perhaps genes), constituting chromosomes, in the cells of the onion. (*From Belling, Univ. Calif. Publ. Bot.* 16.)

individuality, in that the genes in them differ from those of other chromosomes, and the differences persist with only occasional disturbance. Since, however, there are two genes of each kind, there are two chromosomes of each kind. The two chromosomes containing like genes have these genes placed in the same order, so that if the tenth gene in one of them has to do with color of body, the tenth gene in the other likewise is related to body color. This correspondence of the genes extends throughout the twin chromosomes, so that if the two chromosomes were laid side by side, as they are in Fig. 20, matching genes would be everywhere side by side.

[1] Processes described in Chap. VII sometimes lead to the duplication of certain genes, not of others, so that the number of different kinds of genes may be less than half the total number of genes.

From the twin relationship between chromosomes it follows that the number of chromosomes in a cell must ordinarily be an even one. There is an exception in certain animals in which one sex has an odd number of chromosomes; but even in these species the arrangement by couples extends as a rule to all chromosomes but one. The number of chromosomes is the same in all cells of the same individual, and in all individuals of the same species (excepting sex differences), but differs in different species. Very few animals have less than four pairs, and not many have more than 30 pairs. Since there are hundreds of thousands of species, it is obvious that many species have the same number of chromosomes; their genes, however, are always to some extent different.

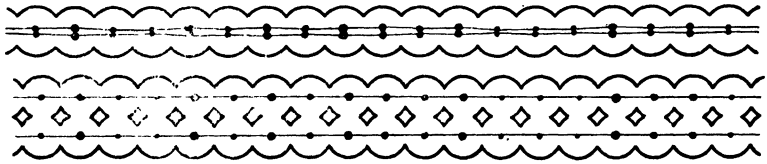


FIG. 21.—Diagram of duplication of genes and division of a chromosome.

Multiplication of Genes.—One of the most important of the attributes of genes is their remarkable ability to produce other genes like themselves. Since every cell of an animal or plant contains in its chromosomes a complete set of genes, and since the organism sprang from a single cell, it is obvious that there must be an extensive multiplication of the genes. No traces of the gene-duplication can be seen until early in the process of cell division or mitosis. At that time the chromosomes are in the form of long slender threads, with the genes presumably (the visible nodules certainly) more or less widely spaced though still connected by nongenic material. Each gene produces probably in a very short time another gene like itself. The duplicated genes lie side by side, and in the aggregate they effect a doubling of the whole chromosome (Fig. 21). The double thread gives the appearance of a splitting of the chromosome, and the process just described is commonly referred to as chromosome division. The real nature of the change, however, is probably much better indicated by calling it a duplication. The genes of all chromosomes in a cell duplicate themselves simultane-

ously, so that temporarily there are twice as many chromosomes in the cell—four of each general type instead of the usual two. With the division of the cell body, one of each two chromosomes resulting from the duplication process goes to each daughter cell. Each daughter cell thus comes to possess exactly the same collection of genes, contained in the same sorts of chromosomes, and arranged in exactly the same order in each chromosome, as did the parent cell.

It is owing to this precise duplication of genes, repeated over and over, without disturbance of the chromosome structure, that all the cells of an organism are hereditarily alike. The reason why the cells in different parts of an animal or plant produce different structures lies, in the opinion of most geneticists, not in the genes they contain, but chiefly in their relative positions.

Meiosis.—Early in the development of most animals, certain cells, either because of their position or owing to something which they contain, are set aside as germ cells. In these the behavior of the genes and chromosomes is eventually very different from that in body cells. The remarkable difference is that the germ cells undergo one division of their cell bodies without a corresponding duplication of their genes, which results in a reduction of the number of genes per cell by exactly one-half. This reduction is effected in a very precise way as follows. At a certain stage, the two genes of each similar pair approach one another and lie side by side. In the aggregate, this approach effects a pairing of each two homologous chromosomes, which lie parallel to one another throughout their length, with homologous genes at the same level (Fig. 22). Double threads are thus produced which resemble the double threads in a body cell preparing to divide, but in the germ cells they are due to a pairing of distinct chromosomes instead of a duplication of one chromosome as in the body cells.

Each of the two paired chromosomes becomes duplicated, by a duplication of all the genes in them, producing a four-parted chromosomal body or tetrad. The germ cell now divides twice in quick succession, and in this double division the tetrads are all separated into their four component parts. Each mature germ cell receives one, and only one, of these parts. As a consequence of this partitioning of the tetrads, there is only one

gene of each kind, hence only one chromosome of each kind, in each mature reproductive cell, instead of two that are present in each body cell. When egg and spermatozoon unite in fertilization, each introducing a single gene of each kind, the double number of genes and chromosomes is restored, so that the new individual derived from them has the usual duplex composition.

The importance of this process for the general permanence of the species can hardly be overestimated, or even overstated; for it insures that every germ cell shall carry the same general kinds of genes that the species possesses. Were there any other mechanism by which the number of genes were reduced to half in the germ cells, almost certainly the great majority of mature germ cells would carry collections of genes different from that

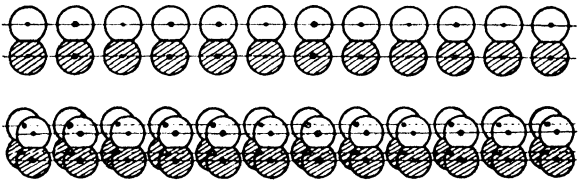


FIG. 22.—Pairing of homologous genes and hence of homologous chromosomes in meiosis. Below, each chromosome has become duplicated to form a tetrad.

pertaining to the species. The pairing of the homologous genes (and chromosomes) and their subsequent separation to different germ cells, which is the essence of meiosis, is what preserves the genes in the same type of aggregation in the germ cells as in the individual which produces them.

Chromosome Differences between Sexes.—Although genes and chromosomes ordinarily exist in pairs of homologues, there is one situation, already mentioned, in which a chromosome is not thus paired. In many animals the male has only one chromosome of a certain kind of which the female has two. Such chromosomes have been named X chromosomes. In a smaller number of species, mainly belonging to other groups in the classification, the female has only one chromosome of a given kind of which the male has two. In recognition of the reversal of the relations of the two sexes, these latter chromosomes are called Z chromosomes.

In the sex which has only one chromosome of this particular kind, the single chromosome can not pair with another chromo-

some in meiosis. In one of the two divisions this single chromosome goes to one cell, while the other cell receives no chromosome of this kind. There are thus two kinds of germ cells, approximately half of them possessing the unmatched chromosome, the other half lacking it. In some groups of animals there are two kinds of spermatozoa, in other groups two kinds of eggs.

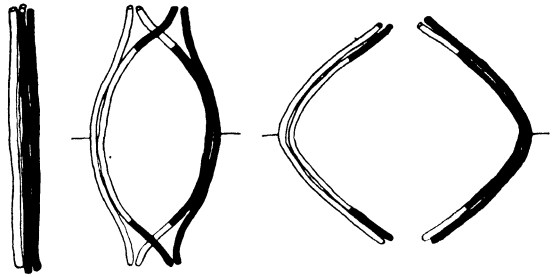


FIG. 23.—Diagram of a tetrad and exchange (crossing over) between its parts in meiosis. Black = paternal; white = maternal. Crossing over occurs between only two of the strands at any one level.

The important consequence of this arrangement is that the sex which has but one of these chromosomes receives it from only one of its parents, while the sex that has two of them receives one such chromosome from each parent. Certain special features of evolution depend on this distinction between the sexes.

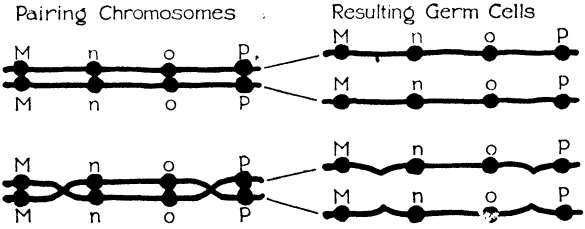


FIG. 24.—Crossing over between chromosomes having identical genes. The germ cells produced after crossing over (below) are exactly the same as those produced without crossing over (above).

Crossing Over.—While the chromosomes of the germ cells are in their four strand stage (Fig. 23) they frequently, perhaps usually, exchange some of their genes. A block of genes forming a segment of one chromosome passes over to the other chromosome, while the corresponding genes lying at the same level in the second chromosome take their place in the first. The number

of genes thus exchanging places is variable. If the exchange takes place at an end of the chromosomes, the genes involved may be very few. If segments out of the middle of the chromo-

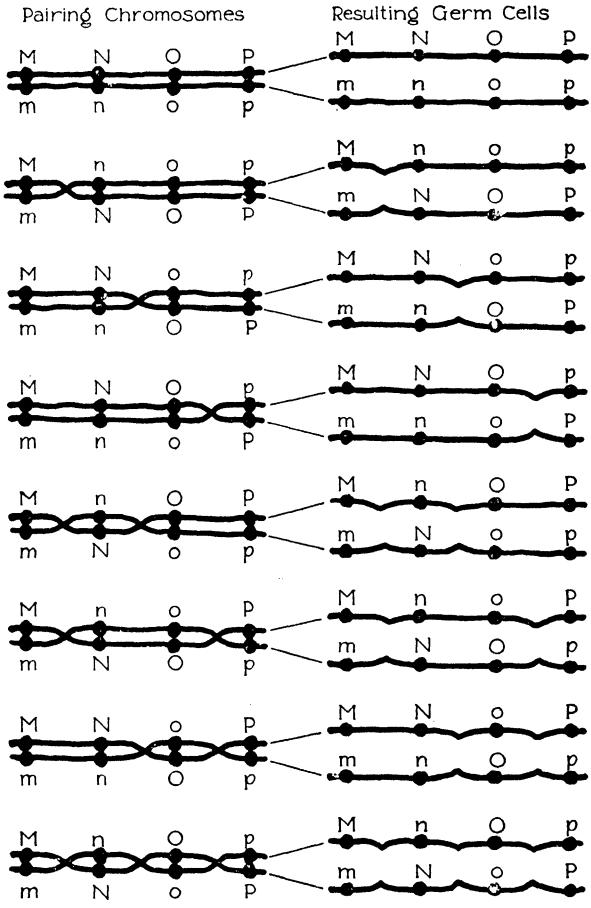


FIG. 25.—Crossing over between chromosomes having unlike genes. With four pairs of unlike genes, 16 different combinations in the germ cells may result, depending on where the exchanges between the chromosomes take place.

somes are interchanged, there are lower limits below which the number seldom falls. In Drosophila, the mean size of the transposed groups of genes amounts to at least one-third of the chromosomes, while the minimum size is probably not over one-twelfth. Two or three nonadjacent groups of genes in the same chromo-

somes may trade places at the same time, but such simultaneous exchanges are less frequent.

If the genes in the two homologous chromosomes are all exactly alike (Fig. 24), this exchange, or crossing over as it is called, produces no change in the constitution of the chromosomes. If, however, the genes are somewhat different in the homologous chromosomes (Fig. 25), crossing over results in two chromosomes having each a collection of genes differing from that which either chromosome possessed before. In the two chromosomes together exactly the same genes are present, but their distribution between the chromosomes is altered. As a result, the germ cells to which the chromosomes are distributed in meiosis have different aggregates of genes, and the individuals developing from these germ cells contain different groups of genes. The important consequence of crossing over is that genes are not eternally bound up with the same other genes in chromosomes. At every generation they are given an opportunity to part company with their old associates and join new ones—a fact of exceeding significance for evolution.

Types of Change in Heredity Mechanism.—Here is the mechanism by which organisms of the more complex classes—those employing bisexual reproduction—maintain their constitutions. Here, then, is the place to look for those persistent modifications which constitute evolution. Such modifications may arise in two essentially different ways. Changes of one type occur as a result of the ordinary operations of the mechanism, and these may be expected at any time or all of the time. Since alteration of individuals by this method can not occur unless there have been changes of another sort in advance of it, these modifications may be regarded as secondary. The primary changes occur at irregular, perhaps infrequent, intervals, and are alterations of the units of which the mechanism is composed, or of their position in relation to one another. Secondary modifications are described as part of the operations of heredity in the next chapter, primary changes in Chap. VII.

CHAPTER VI

RECOMBINATION OF GENES AND ITS BEARING ON EVOLUTION

> The revolutionary effects of Mendelism will be seen to flow from the particulate character of the hereditary elements . . . It is a remarkable fact that had any thinker in the middle of the nineteenth century undertaken, as a piece of abstract and theoretical analysis, the task of constructing a particulate theory of inheritance, he would have been led, on the basis of a few very simple assumptions, to produce a system identical with the modern scheme of Mendelian or factorial inheritance. R. A. FISHER, 1930.

Strictly speaking, all the phenomena of heredity have a bearing on the process of evolution. This is particularly true if evolution be defined simply as change in the mechanism of inheritance, or as the occurrence of inherited modifications. Such a definition is justified from a laboratory point of view and focuses attention upon a feature of evolution that was long unknown or ignored, namely, the distinction between two fundamentally different types of variation. However, since some of the great puzzles of evolution, and most of its popular interest, concern the change as it has occurred in nature, where survival has been of as much importance as the origin of modifications, the operations of the heredity mechanism are of very unequal value as contributors to the process. A clear notion of the relation of heredity to this long-range evolution may be had by laying emphasis on the phenomena of widespread occurrence, and upon the more specialized ones only when they may have served an evolutionary end with relative promptness. In front rank among these phenomena, as a continuing source of change, is the rearrangement of the genes.

Recombination of Homologous Genes.—One of the simplest and most far-reaching of the features of heredity is the particulate nature of the process, resulting from the relative independence of the genes, and the consequent almost endless number of ways in which they may be combined. An organism is made up of a

host of these distinct units which may be rattled and thrown like dice, always, however, with certain restrictions which prevent most of their combinations from being fatal. How the genes operate will be understood from the description of the basis of evolution in the preceding chapter.

As a first consideration, the genes exist mostly in pairs of twins. For every gene in a given cell, there is another gene very similar to it, and not infrequently identical with it, in the same cell. These two genes are in different chromosomes, along with numerous other genes which are likewise similar by twos. The two homologous chromosomes containing similar genes regularly go to different germ cells in meiosis. As a consequence of this separation, no germ cell gets more than one of the genes of a twin pair, and no germ cell lacks any particular kind of gene. Every mature germ cell has one gene of every kind, and only one. This is the important restriction referred to above as preventing fatal recombinations. If a germ cell could lack any kind of gene, and such a germ cell were to be fertilized by another lacking the same kind, a defective combination would result that in most instances would be unable to survive. The regular separation of the twin chromosomes and genes, one of each kind to each germ cell, prevents most such losses.

Within the limitation that each germ cell must have one gene of each kind, there is opportunity for great variety. The two genes of one kind may not be quite alike. Indeed, they may often be any two of a considerable number that are slightly different from one another. Thus, in the vinegar fly Drosophila one particular spot in the X chromosome which has to do with eye color is occupied by thirteen slightly different genes in the chromosomes of the various individual flies. Each of these genes, in conjunction with other genes in the flies, gives rise to a different eye color. No one fly may contain more than two of these genes, but it may contain any two. Consequently, taking the species as a whole, this group of thirteen genes may exist in $13 + 12 + 11 + 10 + 9 + 8 + 7 + 6 + 5 + 4 + 3 + 2 + 1 = 91$ different combinations, of two genes each. Those who do not understand the mathematics of combinations will readily see how this number is arrived at in the chart in Fig. 26. Other organisms, including mice, rabbits, guinea pigs, locusts, beans, snapdragons and corn, also have several different genes occupying

the same locus in homologous chromosomes of different individuals. It seems likely that every locus is capable of lodging several unlike genes in different homologous chromosomes, and probably most loci have done so, even though some of the alternative genes have not survived to the present. This existence of several or many somewhat different genes at some or all of the positions in the chromosomes results in a degree of variation which depends on the number of genes in each series. If only

aa	bb	cc	dd	ee	ff	gg
ab	bc	cd	de	ef	fg	gh
ac	bd	ce	df	eg	fh	gi
ad	be	cf	dg	eh	fi	gj
ae	bf	cg	dh	ei	fj	gk
af	bg	ch	di	ej	fk	gl
ag	bh	ci	dj	ek	fl	gm
ah	bi	cj	dk	el	fm	
ai	bj	ck	dl	em		hh
aj	bk	cl	dm		ii	hi
ak	bl	cm		jj	ij	hj
al	bm		kk	jk	ik	hk
am		ll	kl	jl	il	hl
	mm	lm	km	jm	im	hm

FIG. 26. The various combinations into which 13 genes may enter, taken two at a time.

two genes exist in a series, they can be combined in $2 + 1 = 3$ ways; three genes at a given locus may constitute $3 + 2 + 1 = 6$ combinations of two genes each; five genes may enter into $5 + 4 + 3 + 2 + 1 = 15$ combinations; eight genes into $8 + 7 + 6 + 5 + 4 + 3 + 2 + 1 = 36$ combinations; and so on.

Recombination of Nonhomologous Genes.—The above considerations apply to genes occupying the same locus in corresponding chromosomes of different individuals. Much greater variety is secured through recombination of genes relating to different characters. When two genes are in different pairs of chromosomes, they enter into new combinations with the utmost

freedom, for the chromosomes are usually quite independent of one another in their distribution at meiosis. Though the two chromosomes of one pair must go to different cells, they do not in any way influence the distribution of the other pairs. Thus, if in one pair of chromosomes in the various individuals of the species there are three genes of one general kind, capable of being combined in six ways as explained above, and in another pair of chromosomes there are four somewhat different genes at a given locus capable of being combined in ten ways, these two groups of genes alone provide 6×10 different combinations. For every group of homologous genes added to the calculation, the total number of possible combinations is *multiplied* by the number of combinations of the added genes. Any position that is occupied by only one kind of gene in all homologous chromosomes throughout the species contributes nothing to this variability, since all individuals will be alike with respect to it.

Now, most organisms must possess several thousand genes. If this number be taken as 6000 (3000 pairs), and if it be assumed that only 1 per cent of the 3000 loci in the chromosomes are occupied by more than one kind of gene, and that the number of kinds of genes at one locus is not in any case more than two, the number of possible combinations of genes in the species would still amount to the staggering total of 3^{30} or over 200,000 billions. It is obvious that such a situation offers abundant material for evolution.

Genes in the Same Pair of Chromosomes.—It may be objected that the above discussion assumes complete independence of the several groups of homologous genes, and that to possess such independence each group would have to be in a different pair of chromosomes from all the others. In the calculation just made, which involved 30 loci, this objection would imply that there must be at least 30 pairs of chromosomes, and most organisms do not have so many. The objection is, however, not well founded. In the long run, the occurrence of two or more series of homologous genes in the same chromosomes does not interfere with their recombination in all possible ways. It is true, there is some interference for a few generations. During these few generations the genes that are together tend to stay together, which means simply that they stay together more often than not. However, when they do separate and exchange places in crossing

over, there is started a new combination which persists as tenaciously in later generations as the original combination did. A calculation involving the laws of chance shows that in a relatively small number of generations—15 or 20—the new combination is not appreciably less frequent than the old one. In hybridization experiments, which usually extend over only a few generations, the linkage of two or more pairs of genes in the same pair of chromosomes has an important influence on the relative numbers of different kinds of individuals; but in evolution, which involves thousands of generations, recombination may be regarded as quite free notwithstanding linkage in chromosomes.

Restrictions upon Freedom of Assortment.—The conclusion just reached applies only to species in which there is regularly, or at least frequently, biparental reproduction. This is the situation in nearly all animals above the protozoa, and may occur in most of that group also. Many plants are also biparental. When, however, reproduction is chiefly or solely vegetative (asexual), recombination of genes is greatly restricted. Self-fertilizing hermaphroditic organisms (which are mostly plants), and parthenogenetic ones (which are found among both plants and animals), likewise exhibit little of the recombination described above. However, even self-fertilizing organisms occasionally cross, and many parthenogenetic species also at times employ bisexual reproduction. The limitations put upon free recombination of genes by the mode of reproduction are therefore less severe than they at first sight appear.

Another means of diminishing freedom of assortment of genes is found in the failure of certain linkages in the chromosomes to break. Thus, in the small chromosome pair of Drosophila, which contains only three known mutant genes, crossing over is practically nonexistent. Also in male Drosophila there is rarely any crossing over even in the larger chromosomes under ordinary conditions, though the exchange can be induced by high temperature and X rays. In other organisms in which linkage has been studied, practically all the known genes have, at one time or another, broken their associations with every other gene.

The net conclusion regarding recombination of genes is that, for much the greater part of the living world, and for periods long enough to be of significance in evolution, the assortment is free and untrammeled. In other words, organisms, either as indi-

viduals or as species, are assemblages of discrete units, their inherited characteristics, which are capable of an immense amount of rearrangement. This is what is meant by the term particulate as applied to heredity.

Characteristic Ratios of Gene Combinations.—Under the circumstances just outlined, certain combinations of genes must exist in a certain proportion of individuals, depending on how abundant the several genes are in the population. If it be assumed that all kinds of individuals are equally fertile, that the combinations of genes in the germ cells are contrived wholly at random, that the germ cells containing the various gene combinations unite with one another fortuitously, and that all the resulting individuals survive or that the several combinations survive in proportion to their numbers, there must be a fixed ratio of the possible kinds of individuals in each generation. Only a simple instance of these operations of chance may be advantageously used to illustrate the point. If two genes of a pair, *A* and *a*, are equally abundant in a population that employs biparental reproduction, then, under the stipulations of chance and proportionality named, it would be expected that one-fourth of the population would be of the composition *AA*, one-half *Aa* and one-fourth *aa*. Furthermore, under the same stipulations, it would be expected that the ratio of these three kinds of individuals would remain indefinitely 1:2:1. If some temporary disturbance of the fortuitous events should increase the relative numbers of *AA* and *aa* individuals and decrease the *Aa* type, but leave the genes *A* and *a* equally numerous, and then the system of purely random events should return, the ratio of the three kinds of individuals would promptly return to 1:2:1. All that is necessary to produce this ratio is equal numbers of the genes *A* and *a* in the population, equal fertility and random combination and survival.

The above is only a special case of a more general rule. Since populations seldom have equal numbers of two alternative genes at any given locus in the chromosomes, it is worth while to state the general proposition. Usually the alternative genes are very unequally numerous. When a new gene, let us say *a*, is first introduced into a population previously having only *A* at that locus, only a few chromosomes and individuals contain *a*. Under these conditions most individuals are *AA*, a moderate or small

number *Aa*, while *aa* individuals are rare or absent. The precis expected numbers can be calculated if the relative frequencie of *A* and *a* genes are known. If the proportion of the gene *A* in the population is represented by the fraction p, and th proportion of gene *a* by q, such that $p + q = 1$, then the fractio of the population having the constitution *AA* should be p^2, th fraction having the composition *Aa* should be 2pq, whil the *aa* individuals should be the fraction q^2 of the total. To stat the results concretely, suppose that 0.9 of the chromosomes of certain kind in a species contain *A*, while 0.1 contain *a* at th corresponding locus. If the distribution, survival, etc., of th genes are all random, 0.81 of the population should be *AA* 0.18 *Aa*, and 0.01 *aa*.

It must be remembered that the population referred to canno be the entire membership of any species. It cannot even be an considerable fraction of a well-established species. In thes large units there could not be random mating; mere distance if nothing else, would prevent it. The population to whic such a formula relates must be small enough that random matin may actually occur throughout it; but it must also be larg enough that all possible types of mating may occur with certainty and with their expected frequencies. The situation describe is thus an ideal one. What, it may be inquired, is the advantag of calculating the consequences of a contingency that neve occurs? The answer is twofold: first, it emphasizes that in th absence of any known controlling agency the composition of a species is nevertheless definitely determined; and second, i illustrates the basis of the conclusion that when a species i nature does not conform to the expectation due to chance, i may safely be assumed that some other factor is working.

The proportion of types so far described depends upon propaga tion through two parents, a requirement which is met in most o the higher organisms. When, as in a few plants (beans, wheat) self-fertilization regularly occurs, there is a steady progres toward homozygous individuals. An occasional cross-fertiliza tion, or the introduction now and then of an alternative gene would cause some heterozygotes (*Aa*) to arise; but their numbe would be reduced by one-half in each succeeding generation o self-fertilization. For the homozygotes (*AA* and *aa*) woul produce nothing but homozygotes, and half of the progeny o

heterozygotes would be homozygotes. Theoretically the heterozygotes should never quite disappear, but actually they would do so, since not all individuals can survive, and sooner or later the attenuated heterozygous group would all be included among the losers.

Genes in X or Z Chromosomes.—A special situation with respect to recombinations of genes exists in those chromosomes most closely related to sex. As already explained, in some animals (mammals including man, most insects, some fishes) the female has two X chromosomes, the male only one. The spermatozoa of the male are of two kinds, one possessing an X chromosome, the other lacking it, while the eggs of the female are all alike in containing one X. The X chromosomes are sex-determining, and sex is fixed at the time of fertilization of the egg; for, if the spermatozoon which unites with the egg contains an X chromosome, the fertilized egg will contain two, and will develop into a female, while if the entering spermatozoon has no X chromosome, the fertilized egg will contain only one and will produce a male.

In a smaller number of other animals (birds, butterflies and moths, and some fishes), sex is likewise determined by chromosomes, but these are known as Z chromosomes because the male possesses two of them and the female only one. An egg without a Z chromosome yields a female, while one possessing a Z chromosome develops into a male, since in any case the spermatozoon which fertilizes it introduces a Z chromosome.

The restraint put upon recombination of genes arises from the fact that one sex possesses only one chromosome of the sex-determining kind, and hence only one gene of each kind contained in that chromosome. There can be no recombination of these genes in that sex. A male mammal receives all his X chromosome genes (sex-linked genes, they are called) in a single block from his mother, and he transmits them without any rearrangement to each of his daughters. A female moth receives all her Z chromosome (likewise sex-linked) genes in a group from her father and transmits them in an identical group to each of her sons.

While this peculiarity of sex-linked genes has a very striking effect on the collections of genes in the individuals of a genetic experiment, it does not restrict the recombinations that bring

about evolution. The reason for this is that the X and Z chromosomes pass from one sex to the other in successive generations. An X chromosome in a male fly experiences no rearrangement of its genes in that fly; but in the next generation it is in a female fly, in company with another X chromosome, and there through crossing over a redistribution may take place. The same possibility exists in the Z chromosome, for such a chromosome passes from a female in one generation always to a male in the next.

CHAPTER VII

PRIMARY SOURCES OF VARIATION

> The basic change factor is gene mutation, the occasional failure of precise duplication. . . . It only requires a very moderate mutation rate in a large population for the number of unfixed loci to become enormous. SEWALL WRIGHT, 1931.

A considerable amount of variability within a species we have seen to flow from the recombinations of different genes. Every species includes more different kinds of genes than any one individual possesses, and the individuals are made up of combinations of a limited number of these unlike units. While a very large part of evolution may be accounted for in this way, recombination is a solution which creates another problem. How does it come that there are so many unlike genes to recombine? Why, in a given locus of homologous chromosomes of different individuals, is there more than one kind of gene? That can not have been the original condition of the species. By no conceivable natural method of originating species can there have been, from the inception of such a group, individuals which differed with respect to many of their genes. These genes must have become different in the course of the history of the species.

Gene Mutation.—The source of variation among the genes of any locus is obviously a series of changes in the nature of the genes. These changes are called mutations. They are presumably chemical alterations, just as physiological and developmental processes must be chemical. When one gene has become thus modified, it operates, in conjunction with other genes, to produce new characteristics in the organism which contains it. The new characteristics are transmitted to later generations in accordance with the rules of heredity. That is the way in which mutations are discovered. When an organism possesses a trait which is unlike any that its ancestors possessed, and which could not have resulted from any recombination of its ancestral characters, and when this new quality

is handed on to the descendants by recognized methods of heredity, then it is known that a mutation has occurred. The gene itself cannot be seen, hence no change in it can be directly observed; but by its effect on the individual and its descendants, as compared with their ancestors, the existence of a change is demonstrated.

Such changes that are carried along by heredity have been discovered in many kinds of animals and plants. Hundreds of them have arisen under observation in one species, the vinegar fly Drosophila. They have produced dozens of changes in the color of the eyes, which in the wild-type fly are of an intense red. Other dozens of them have affected the shape of the wings. Many of them have altered the color of the body, which is ordinarily of a grayish brown. A number of mutations have changed the spines on the body, by cutting them short, crumpling them, dividing them at the tips, or even omitting them. The antennae, legs, ocelli (simple eyes) and internal organs have all been changed by mutations. Corn has likewise experienced a large number of modifications affecting the color, shape and content of the grains, the form and color of the leaves, the number of ears per stalk, the shape of the tassel, etc. Rats, mice, rabbits and guinea pigs have undergone such changes in the color of the eye and color and length of the fur. Many garden plants, among them morning-glories, primulas, snapdragons and sweet peas have exhibited such changes, as have also the farm crops wheat, barley, oats, rye and beans. In fact, every organism that has been extensively reared in laboratories or greenhouses or at experiment stations under careful observation has given evidence of mutations.

The changes effected by gene mutations are of a wide variety. The ones named above are all structural or relate to color, and are easily detected. Some discovered mutations affect physiological properties, like the protein content of corn. There is no sharp distinction between these two kinds, for every structural mutation must also be physiological, for structures arise through physiological processes. Moreover, a mutation that results in altered structure may have other physiological effects not connected with the development of that particular structure. Thus, nearly all of the hundreds of gene mutations in Drosophila which are recognized by structure or color affect (unfavorably)

the length of life and fertility of the flies. The chief reason for drawing attention to the distinction between structural and physiological effects of mutation is to point out that in all probability the mutations we know best are not those of most concern to the organisms. Mutations affecting growth, fertility, or resistance to disease would seldom be detected by ordinary genetic experiments, yet could influence their possessors immeasurably more than would those modifying eye color or length



FIG. 27.—Habit of growth of *Oenothera lamarckiana* (left) and *Oenothera gigas*. (*Photograph by Professor B. M. Davis.*)

of spines. The validity of the applications of evolution theory often depends on a correct judgment regarding the value of mutations to their possessors, and it is likely that this judgment has often been wrong.

Whole Chromosome Aberrations.—Besides mutations affecting individual genes, there are genetic changes involving the chromosome content of cells or the arrangement and number of genes in the chromosomes—all without any change in any specific gene. Changes involving entire chromosomes are considered first. One of the simplest of these modifications, and the most likely to lead at once to successful evolutionary change, is a doubling of the chromosome number. The doubling apparently

occurs, in the forms best known, immediately after an egg is fertilized, at the very beginning of development. Presumably, after the chromosomes have become duplicated the cell division fails to continue, and a single cell with twice the usual number of chromosomes and genes results. A variety of the evening primrose, *Oenothera gigas*, has arisen several times in pedigreed cultures from *Oenothera lamarckiana*, by this process of chromo-

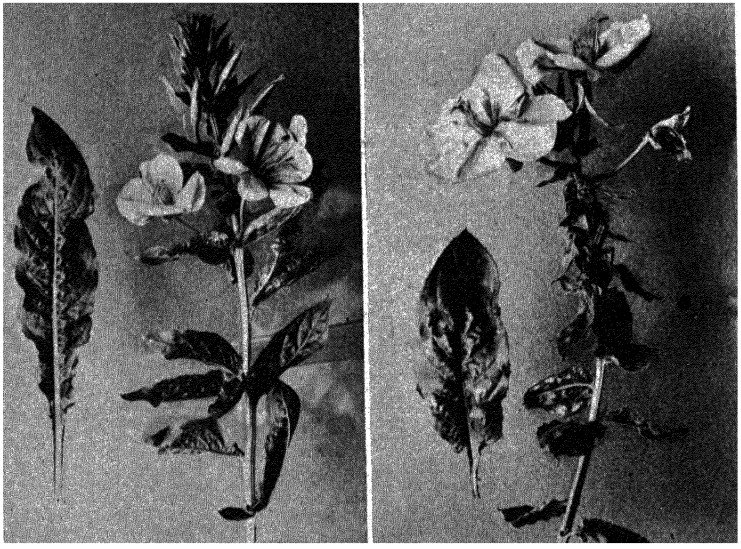


FIG. 28.—Buds, flowers, seed capsules and leaves of *Oenothera lamarckiana* (left) and *Oenothera gigas*. (*Photograph by Professor B. M. Davis.*)

some doubling. The former has 28 chromosomes, the latter 14. *O. gigas* is a giant form, but since its parts are not all equally affected by the increase of size there is at least an appearance of qualitative change. The habit of growth, seed capsules, leaves and buds are affected (Figs. 27, 28, 29). Other changes due to chromosome doubling have been found in the Jimson weed Datura, and increase of size is again the principal visible result. A presumable case of the same phenomenon occurs in the shepherd's purse Bursa, which was mentioned in Chap. III. One species has 32 chromosomes, another 16. In the species with 32 chromosomes, a certain gene affecting the shape of the seed capsule has been proved by hybridization experiments to

be present four times instead of the usual two. It is reasonable to conclude that this condition arose by a doubling of the 16 chromosomes, in two of which this gene was already present. The existence of species having such double numbers of chromosomes is further indicated by the experimental production of mutations by irradiation, as described later in this chapter. Such experimental mutations are readily brought to light in the $2n$[1] species, but not in the $4n$ species. The reason is that, to show in a $4n$ species, two mutations would usually have to occur



FIG. 29.—Rosettes of *Oenothera lamarckiana* (left) and *Oenothera gigas*. (*Photograph by Professor B. M. Davis.*)

simultaneously, whereas in a $2n$ species a single mutation is readily discovered. The simultaneous occurrence of two uncommon events should be very rare.

Plants having one and one-half times the usual number of chromosomes ($3n$) have sometimes occurred, and have been produced by crossing those having the double number ($4n$) with those having the regular $2n$ number. *Oenothera semigigas* may be produced by crossing *gigas* with *lamarckiana*, and it has the expected 21 chromosomes. It also arises spontaneously, somewhat more frequently than *gigas* does. Such forms differ visibly from their parent type chiefly in their larger size.

Variant individuals with only half the usual chromosome group have been produced, in tobacco, for example. They are usually less vigorous and somewhat dwarfed, and have reduced

[1] The number of chromosomes in a mature germ cell is designated n. Hence the individuals are $2n$, and any individuals or species resulting from the doubling just described are said to be $4n$.

fertility because of irregularities in the distribution of the chromosomes in meiosis.

A very different sort of new type is produced when only one of the kinds of chromosomes exists in unusual number. This

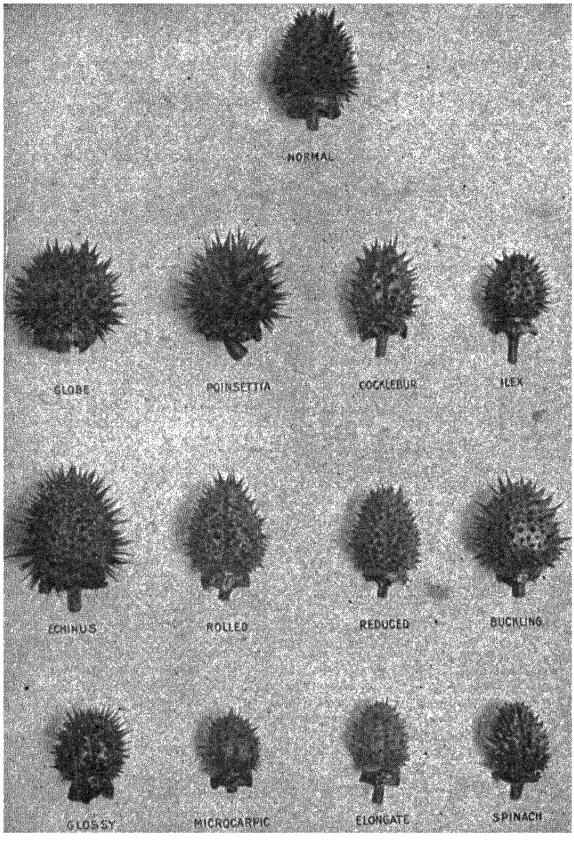


FIG. 30.—Seed capsule of normal $2n$ Datura at top, with those of twelve $2n + 1$ varieties below. (*From Blakeslee, in Journal of Heredity.*)

sort of change, which is fairly common, will be illustrated by an example in which there are three chromosomes of one kind, and two of each of the rest ($2n + 1$). An excellent series of these has been obtained by Blakeslee and his collaborators in Datura. The Jimson weed normally has 24 chromosomes, of 12 kinds. When in some manner there come to be three chromosomes of one kind, or a total of 25, the plant is altered with respect to the

seed capsule, shape of leaf, or habit of growth. Twelve unlike varieties (Fig. 30) involving these characters have appeared, and cytological studies indicate that probably the extra chromosome is of a different pair in each of the twelve. Such variants exhibit lowered fertility as would be expected. Relative stability of these new types would depend on matching up the extra chromosome with another like itself, but even such a plant should produce some abortive pollen or ovules.

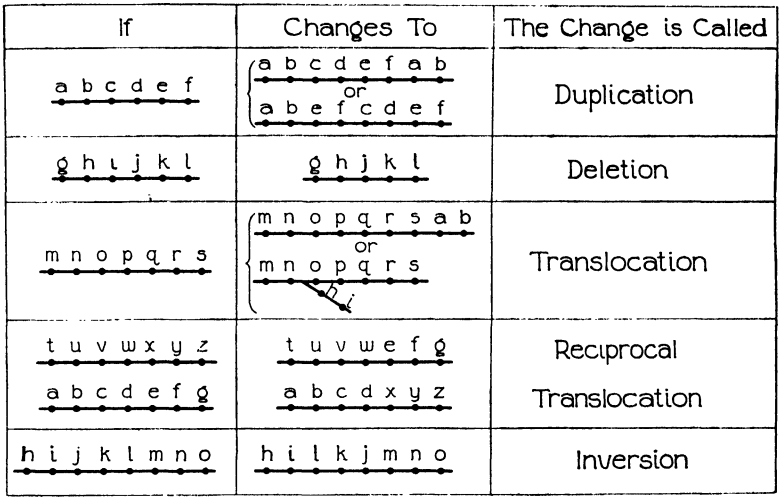


FIG. 31.—Diagrams defining the changes produced by redistribution or rearrangement of fractions of chromosomes.

Various other chromosome modifications are possible. Several additional chromosomes may occur, or there may be extra chromosomes of some kinds and missing members of other kinds. When these abnormalities are multiplied, their difficulties are likewise multiplied. At their best such abnormal forms produce but few functional germ cells; at their worst the chromosome combination proves fatal to the individual that possesses it.

Chromosome Fragments.—Not infrequently it occurs that chromosomes are broken, and then various things may happen to the pieces. A fragment containing certain genes may become attached to an entire homologous chromosome, that is, to a chromosome containing the same genes as the fragment does along with the other genes belonging in that chromosome. Since the whole chromosome and its attached fragment behave as a

unit, there has been produced, in effect, a new chromosome in which certain genes occur twice instead of once as is usual. The union of a chromosome fragment to a whole chromosome of the same kind is called duplication (Fig. 31), from the double representation of the genes occurring in the added piece.

Complementary to this duplication of genes in a chromosome is the absence of them from the chromosome which furnished the shifted fraction. A number of similar losses have arisen in genetic experiments, and have been artificially induced by X-ray treatment. They are known as deletions. They need not involve merely the end of a chromosome, but may occur at any point in its length. Large deletions may be detected cytologically, though it is seldom safe to conclude that a shortened chromosome has suffered such a loss unless genetic experiment has shown that certain genes are absent. Small deletions can be detected only by experiment,[1] and exceedingly small ones may escape detection unless some known mutant gene which may be used as a "marker" falls within the region lost, or unless the deletion has an effect of its own apart from the genes eliminated. There is some reason to think that certain effects originally attributed to gene mutation are really due to very small deletions.

Sometimes the fragment removed from one chromosome is attached to another chromosome of a different kind, that is, to a nonhomologous chromosome. A change of this sort is known as a translocation. The name duplication can not be applied in this case, since almost always the added genes would be totally different from any genes in the receiving chromosome. A particularly important form of translocation is a reciprocal transfer, or an exchange of portions between two nonhomologous chromosomes. By means of such reciprocal translocations (Fig. 31) the association of genes with one another in chromosomes can be completely worked over. It is not likely that many exchanges of this kind could take place simultaneously, but a succession of them, if they did not prove fatal, might effect a thoroughgoing rearrangement.

[1] These statements apply to chromosomes as found in most cells. In the salivary glands of the Diptera (flies), however, the chromosomes are enormously enlarged, and what are presumably the genes can be seen as crossbands or disks. In these cells chromosome fragmentation and rearrangement of genes can be discovered by observation.

A somewhat less radical rearrangement of genes occurs in inversion. In this process a fraction of a chromosome is turned around, its ends exchanging places. The gene content of the chromosome is not thereby altered, but their arrangement is changed. An important consequence of inversion is that,

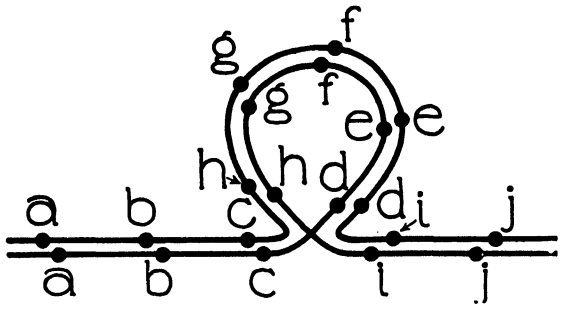


FIG. 32.—Pairing of two chromosomes differing in that the middle region of one is inverted. By a direct loop in one and a reversed loop in the other similar genes are brought together.

when a chromosome thus modified pairs with an unmodified chromosome of the same kind before meiosis, the homologous genes do not lie at the same level. This difficulty can be met only by an asymmetrical coiling of the two chromosomes (Fig. 32), or some similar device. How an inversion arises is not

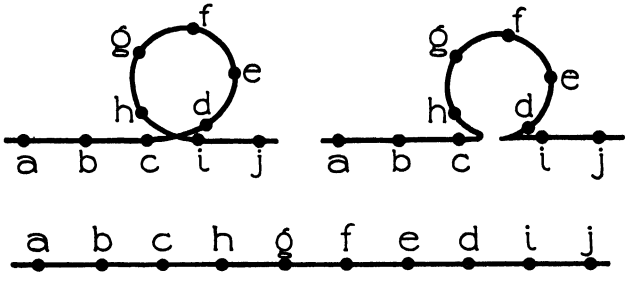


FIG. 33.—Probable mechanism of production of inversions.

known, but not improbably it is due to a loop in the chromosome which, instead of uncoiling, breaks at the point of crossing of the thread before the chromosome straightens out (Fig. 33).

While much of what is known regarding genetic change through chromosome fragmentation has been discovered in the vinegar

fly Drosophila, enough of it has been confirmed in other species to suggest that it may be a fairly general process. If successful evolution can be derived from it, therefore, it is legitimate to speculate upon its possibilities in any or all of the higher animals or plants.

Evolution without Genes.—While the bulk of the phenomena of evolution must depend upon changes in genes or their combinations or arrangements, there is opportunity for a minor amount of it through other means. If any rather permanent and transmissible qualities of organisms owe their existence to objects outside the nucleus, their mode of change could be quite different from that of gene-determined characters. The principal known seat of such modifications is the plastids, small bodies in the outer protoplasm which give the green color to the leaves of higher plants and other colors to some flowers and fruits. The plastids are more or less autonomous, multiplying by direct division. They are carried over from one generation to the next through the egg only in most plants, but through both egg and pollen tube in at least one species. Changes occurring in plastids would result in evolution of a somewhat different sort from that occasioned by gene mutations or chromosome aberrations.

Causes of Mutation: Early Views.—Recognizing that the primary sources of variation in organisms are mutations of genes and various structural or numerical readjustments of chromosomes, we must now seek the reasons for the occurrence of such changes. Views on this question have changed materially since the evolution doctrine was first seriously proposed. Historically the earliest view was that the environmental agencies are responsible, including in that category the functional activities of animals or plants which, though internal, are usually responsive to external stimuli, and in any case are external to the hereditary units, the genes. It was the thesis of Lamarck, over a century ago, that the bodies of organisms become modified by the use or disuse of their own organs, and that these modifications are inherited. The environment, by influencing the activities of the organs, could, he supposed, have an indirect effect of the same kind. This thesis, which is known as the Lamarckian principle, was in a measure adopted by Charles Darwin when he invented the theory of pangenesis to account for it, and has

had numerous supporters in every generation since. To it was added by various naturalists after Lamarck the idea that environment may produce modifications by *direct* action, and not merely by changing the organism's physiological processes. All such environmental or functional changes were apparently regarded as capable of being transmitted. Darwin, it is true, observed that some variations were transmitted, others not, but it was not clear to him that the difference was inherent in the nature of the variations themselves. Although variations were or were not inherited, as he could see, he did not recognize two fundamentally different categories of modifications, one permanent and one transitory.

The appeal which the Lamarckian principle has made to so many naturalists is doubtless due to the belief that the fitness of organisms for their environment is in some manner explained by its adoption. Just why this conclusion should have been arrived at is not clear when many reactions of living things to agencies about them are far from useful. Moths flying into the flame, or corns forming within shoes, can hardly be regarded as examples of fitness. Production of a tumor in a mouse's skin in response to coal tar, and crown gall in plants probably as a reaction to bacteria, are more recently discovered similar instances. Even a moderate knowledge of physiology should have made it plain that usefulness of responses to the environment was not a priori to be expected. Here is not the place, however, to go far into the question of adaptation, since it must be dealt with in connection with the direction of evolution in a later chapter.

The question of transmission of modifications, or better, the modification of the hereditary units or genes, entirely apart from the usefulness of the modifications, is of immediate importance in a discussion of variation. Fortunately, it is one that can be attacked by the experimental method, and no conclusion not in harmony with the results of such experiments can safely be adopted. Since experiment as a method in biology has grown only gradually, the empirical results of successive decades are not all of equal value. Emphasis must therefore be placed upon recent experiments, though some of the earlier attempts are of interest as indicating the difficulties attending such investigations.

Some Lamarckian Experiments.—It should be understood at the outset that the experiments properly considered under this head are those dealing with agents which affected the soma or body, but presumably could not in any way reach the germ cells directly. Should the modifications effected by these agents be transmitted, it would mean that the body had found some means of communicating a corresponding change to the genes in the germ cells. None of the early Lamarckians knew anything about genes, but it is clear now that the things they believed to occur could have happened only through such an influence upon genes. This is the essence of Lamarckism, and evidence of such somatic influence upon the genes must be looked for in every experiment purporting to prove the Lamarckian factor.

Many decades ago, at a time when experiment in biology was still in its infancy, the studies of Brown-Séquard upon guinea pigs attracted much attention. He operated upon the nervous systems of these animals at several places, and induced in some of the animals marked epileptic responses. A very small percentage of the offspring of these animals, without being operated upon, showed, according to Brown-Séquard's account, the epileptic response. More than half a century later the experiments were repeated by Wrzosek and Maciesza, who verified the production of epilepsy by the operations, and who likewise found epilepsy in a small percentage of their offspring. In addition, however, they observed that the epilepsy of the offspring was very mild as compared with that of the parents, a difference not mentioned by Brown-Séquard, though quite possibly existing in his experiments. Furthermore, Wrzosek and Maciesza were able to get a mild epileptic reaction in a small percentage of guinea pigs whose parents had not been operated upon, thus throwing serious doubt upon the validity of the original experiments.

Repeatedly since then experiments purporting to prove somatic influence upon the genes have been described. A long list of them came from Kammerer in Vienna, but his evidence was never complete enough to satisfy critical biologists. Either the animals he used were not sufficiently studied in advance of the experiments to ascertain just what genes they might possess, or his experiments merely showed that the animals used developed one character in one environment, another character in

another environment, without any persistence of either character, or, as was indicated by repetition of the experiments by others, the treatments of the experimental animals and the controls with which they were compared were inadvertently allowed to differ. Detlefsen, by rotating rats on a turn-table, caused them to perform "circus movements" after the treatment. Somewhat similar movements by some of their untreated offspring were at first regarded as proving a genetic change, but later were attributed to an infection of the inner ear where the mechanism of equilibrium is situated.

Inheritance of Learning.—Inheritance of learning has been several times claimed, notably by Pavlov, though similar experiments by MacDowell and by Vicari showed no inheritance. The Pavlov claim is said to have been informally withdrawn, though no retraction has ever been published. Because of their recent date, the experiments of McDougall on inheritance of learning in rats may well receive particular consideration. The method was to drop rats, one by one, into a tank of water, from which there were two avenues of escape (Fig. 34). One of these, not always the same, was illuminated, the other one dark; but if the rat left by the illuminated passage it received an electric shock. The first purpose of the experiments was to teach the rats to leave invariably by the dark passage, whichever one it was. The number of trials required to attain this result was the measure of the speed of learning. These rats were bred, and from among their offspring, by a method said to be purely random, some individuals were tested for their quickness of learning. These tests were continued over a considerable number of generations, and appeared to show in the end that the time required to learn the correct exit from the tank was materially lessened in the trained line of descent. McDougall believes that the results indicate inheritance of learning, hence the modification of genes through somatic influence. A few other biologists have expressed the view that these experiments

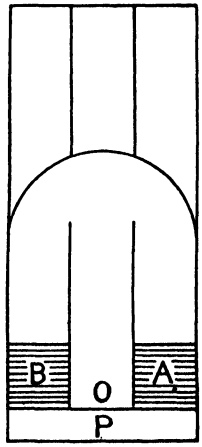


FIG. 34.—Diagram of tank used in McDougall's rat experiments. Rats were put into the water at *O*, and escaped by gangway *A* or *B*. (*From Rhine and McDougall, British Journal of Psychology.*)

have avoided most of the pitfalls of such investigations, but some have pointed out weaknesses in them, as follows.

To be valid, the experiments must have used rats genetically alike; the stimulus applied to them must have been always the same; and there must have been no selection, conscious or unconscious, of rats possessing certain qualities. Sonneborn subjected McDougall's papers to a searching analysis, and found important flaws in his method. With regard to the first requirement, an important comparison is made between stocks obtained from the same supply on dates separated by an interval of seven years. It can hardly be assumed that mutations were lacking in that time. With respect to the second point, McDougall himself states that the intensity of the electric shock varied, and he showed by experiment that the stronger the shock the more quickly the rats learned. There is some internal evidence to show that the period of reduction of the learning time was also a period of intense shocks, and it was suggested that the appearance of increased speed of learning was due to these differences in intensity. Lastly, as to possible selection, McDougall states that all progenies were equally represented among the animals tested in each generation, and that the individuals to be used were selected at random. Sonneborn showed, from a mere consideration of the numbers of animals trained, that the former statement can not be correct; that is, not all progenies were represented at all, hence there was room for selection. How the animals were chosen is not stated, but if the first rat to present itself when the cage was opened was taken, it seemed possible that the most intelligent ones were selected.

A later paper, by Rhine and McDougall (1933), on the continuation of these experiments defends them with some success against the charge of inadvertent selection, since adverse selection did not prevent the descendants of trained rats from continuing to learn faster. It reveals, however, some of the uncertainties of such experiments which lessens one's confidence in their results. For example, a new tank was built, which was supposed to be identical in experimental effects with the old one, but the rats for some reason found it "easier" to solve. The reason for this difference was not discovered. McDougall suggests it may have been better illuminated, but there is no

indication that intensity of illumination was checked in the earlier generations, and it is well known that electric bulbs lose their intensity with age. Then, too, the control (untrained) line showed a progressive improvement in their learning rate over a five- or six-year period. The reason for this change is unknown. McDougall attributes it to fortuitous selection, but if such things can happen without any knowledge of their causes doubt is thrown on the significance of the other changes for which it is possible to suggest a source. Again, there were differences between the trained line and the controls which were presumably not the result of the training. Thus, reduced weight at birth, smaller litters, cannibalism, litter desertion, and certain other defects indicate that some degeneration took place in the trained rats that did not occur in the untrained ones. It can hardly be maintained that the deterioration was a result of the learning, the rats being, like Hamlet's hue of resolution, "sicklied o'er with the pale cast of thought." Something unsuspected had entered to differentiate the two halves of the experiment.

When so many things can happen differently to experimental animals and their controls, which have no relation to the differential treatment and whose cause can only be guessed, it is permissible to wonder whether the one distinction that does seem to arise from, or at least bear a relation to, the treatment really did so. The difficulty is partly inherent in the animals used. They are complex, difficult to analyze. The work of Shepard shows that it may require years of patient and painstaking study to discover what the real basis of learning is in rats. Incorrect conclusions are easily arrived at, and disproved with difficulty. Still, an open mind should be maintained toward McDougall's work. His experiments will doubtless be repeated by others, and if learning is actually transmitted, the same results can be obtained by them.

Transplantation Experiments.—Supposedly somatic effects upon contained genes were obtained by Guthrie when he transplanted the ovary of one fowl into another of a different variety, and then obtained from the receiving fowl offspring like herself instead of like the donor of the ovary. Guthrie overlooked, however, the possibility that the transplant had not grown, and that a remnant of the original ovary, supposedly entirely

removed, had regenerated. Similar transplants in guinea pigs were made by Castle and Phillips, who found that the transplants failed more often than they succeeded and that regeneration was common. They ascertained this by transplanting the new ovary into a strange situation, so that by an autopsy it could be told whether the ovary finally functioning was the transplanted or the regenerated original one. Guthrie neglected to take this precaution, hence all his results are open to the interpretation that frequent regeneration took place.

From the above examples, which are as good as any that have been advanced, it seems clear that no satisfactory evidence that a soma may impress its characteristics, or any characteristics, upon the germ cells within it has ever been obtained. From this and the further fact that the known physiology of organisms includes no mechanism by which a specific influence could be exerted, most biologists have definitely ceased to look to the body as an intermediary in the production of mutations.

Direct Environmental Influence on Genes.—When the environmental agent is one that can reach the germ cells directly, so that modification of the soma is not a necessary step in the process, the artificial induction of mutations rests on a much more plausible basis. The inherent probability that modification of the genes could be thus directly effected led to many attempts. Avery and Blakeslee get mutations in Datura merely by aging the seed, but most attempts have involved temperature, substances soluble in the blood, or radiation. Tower claimed to have induced permanent modification of potato beetles by high or low temperature, provided the temperature was applied during the maturation period of the germ cells. Goldschmidt and others have used high temperature for short periods to produce mutations in Drosophila. Alcohol administered to guinea pigs through the lungs, by inhalation of the vapor, was shown by Stockard to produce abnormalities in the offspring, including reduction or loss of the toes, paralysis, degeneration of the eyes, and loss of general health and vigor. These changes lacked the specific nature of most known mutations, but they continued in the following generations without further alcohol treatment until they were eliminated by the gradual dying out of the affected lines of descent. Pearl likewise treated poultry with alcohol spray, which was inhaled, and thereby caused a

great increase in the mortality of their eggs or embryos. Chicks that escaped this early injury were the most vigorous ones, so that the surviving offspring of alcoholized fowls were noticeably superior.

Mutations Induced by Radiation.—The outstanding production of mutations by artificial means is that done by X rays or radium emanations. X rays had long been used to cause irregularities in the distribution of the chromosomes, but it was not until 1927 that Muller succeeded in obtaining numerous mutations in Drosophila by this method. The modifications

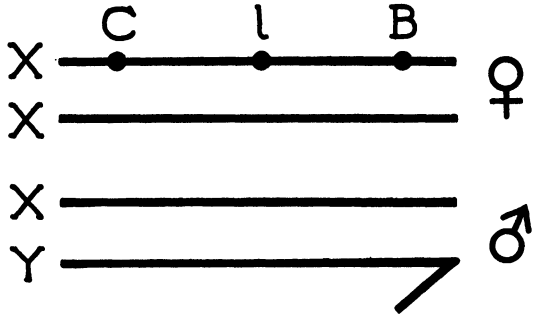


FIG. 35.—The X and Y chromosomes of the so-called *C l B* stock of Drosophila used to detect artificially produced lethal mutations. *B*, gene for bar eye; *C*, crossover factor (perhaps not a gene), preventing exchange between the two X chromosomes; *l*, lethal factor.

most easily discovered are of the class known as lethal, or fatal, mutations; for, while the lethal mutations might be of many kinds, they all had the same result, they killed their possessors under certain circumstances, so that the experimenter knew what result to look for. Lethal mutations in the X chromosome are especially favorable because a male Drosophila, having only one such chromosome, succumbs if a single lethal mutation occurs in the X chromosome. Females are protected by having two X chromosomes; they are killed only if two identical lethal mutations occur, one in each of the X chromosomes, at the same level, which would rarely happen, purely as a result of chance. A special method of recognizing lethal mutations within one generation after their production was devised by Muller, to save a great deal of labor. A stock of flies in which one of the X chromosomes of the female already contained a lethal factor was obtained. In this same X chromosome was the dominant

gene for bar eye (Fig. 35), which visibly marked all flies containing that particular chromosome, also what is called a crossover factor which prevented exchange of parts of the two X chromosomes, so that the lethal gene and the bar gene were always in the same chromosome. Half the eggs of such a female would contain the bar-and-lethal X chromosome, and these could not develop into males because of the lethal. Suppose, now, that a female of this kind had received from her father also an X chromosome containing a lethal gene. The female would survive, unless the lethal from the father happened to be identical with that from her mother, which would be very unlikely. Since, however, both of her X chromosomes contained lethal genes, she could produce no surviving male offspring, a result that could be detected very quickly.

Muller's experiments consisted, therefore, in attempting to produce lethal X chromosome genes in the spermatozoa of males, mating such males to females some of whose eggs would already contain an X chromosome lethal, and obtaining thus fertilized eggs, and from them females, both of whose X chromosomes contained lethals. Such females would produce no male offspring, and every sonless family was evidence that a lethal mutation occurred in one spermatozoon produced by its grandfather. Since lethal mutations occasionally arise spontaneously, proof of artificial production of such mutations would require that more of them occur with treatment than without it. Muller's experiments met this requirement in astounding fashion, for about 150 times as many sonless families occurred after X-ray treatment as in normal families.

Another special chromosome setup has been employed to detect visible mutations, such as eye color or shape of wing. It consists of a stock of Drosophila in the females of which the two X chromosomes adhere to one another (Fig. 36). Without explaining fully how this peculiarity influences sex, it may be pointed out that the sons of such females are like their fathers with respect to sex-linked characters, not like their mothers as is true when the X chromosomes are separate. The advantage of this feature is that, if mutations are produced in the X chromosome of any spermatozoon of a male fly, and the male is mated with a double-X female, this mutation may be detected in the very next generation, instead of a generation later as must

otherwise be necessary. This saving of labor has made it possible to try for such artificial mutations in large numbers. The attempt has been successful, for as many as 7 or 8 per cent of the male progeny of irradiated males have exhibited visible modifications.

Radium treatment was used to induce mutation in Oenothera by Brittingham and in barley by Stadler. In the latter plant there are three stems and heads on each plant, each coming from a rudiment already present in the seed. A mutation occurring

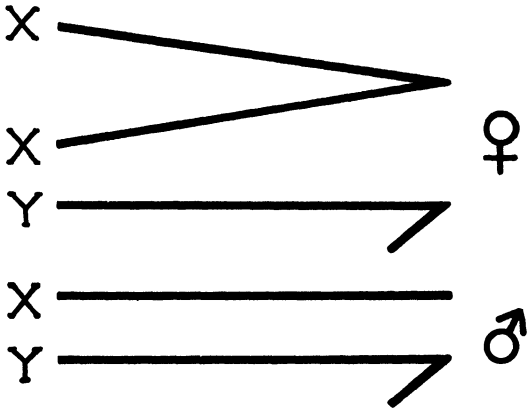


FIG. 36.—The X and Y chromosomes of the attached-X stock of Drosophila used to detect artificially produced visible mutations.

in the egg or pollen nucleus before the seed is formed would affect all three parts of the embryo; but a mutation occurring in the seed would affect only one of them. Stadler irradiated the seeds, allowed the flowers of the plants derived from them to fertilize themselves, and planted grains of the three heads separately. If the progeny from one of the heads were of two kinds, while the other two heads bred true, it was evident that mutation had occurred in the one rudiment in the seed. Since irradiated seeds yielded such mutants more frequently than did untreated seeds, the mutation must be attributed to the treatment.

Genetic tests of the modifications produced by X-ray treatment in Drosophila have shown them to be of different kinds. Many of them are gene mutations, either new ones or repetitions of mutations that had occurred spontaneously before. Others

are deletions, translocations or inversions. Mutations have also been produced in somatic cells by X-ray treatment, resulting in white patches in an otherwise red compound eye. Somatic mutations have no influence on evolution in animals, since no germ cells are derived from the modified cells. They help to show, however, that X-ray-produced mutations are of the same general sort as those that arise spontaneously.

Radiation of other wave lengths has also produced mutation. Heat was first used by Muller and Altenburg to increase the mutation rate in Drosophila, and subsequently by Goldschmidt, Jollos, Plough and Plough and Ives. Extreme temperatures applied for short periods to the larvae effected many such changes. Some of these mutations were duplicates of changes arising naturally before; others were wholly new. A darker body color and abnormal structure of abdomen were repeatedly produced in some of the experiments. Ultraviolet was later used to produce mutations in Drosophila (Altenburg) and in snapdragons (Noethling and Stubbe). Various wave lengths seem thus effective in modifying genes.

Is Radiation a Cause of Mutation in Nature?—The identity of some of the mutations produced by X rays with spontaneous mutations, and the fact that in their general nature all of them were of the kinds being obtained without treatment, raises the question whether natural mutations may not thus be produced. There is a small amount of radiation about the earth at all times, and mutation caused by it might conceivably be a universal phenomenon. Some tests of this possibility were made in situations where the amount of radiation is greater than usual, as by Babcock and Collins in a railway tunnel, and by Hanson and Heys in a carnotite mine. Ionization tests showed that the radiation in these places actually was greater than on the open surface of the earth. In both of these tests flies reared amid the greater radiation, after the manner of Muller's experiments described above, yielded more lethal mutations than did those on the open surface. The differences were not large, however, and statistical calculations showed them not to be wholly conclusive.

Some further doubt is thrown on radiation as the cause of natural mutations by the large number of these which have occurred. It has been shown that the number of lethal mutations

produced by X rays is roughly proportional to the amount of radiant energy used. Muller has used this relation to calculate how much radiation there would have to be to have produced the many mutations that have arisen in Drosophila in the last twenty-odd years, and finds that the radiation actually in existence is less than a thousandth of the required amount. He has considered the possibility that radiant material may be concentrated near the germ cells in the flies, but this has seemed unlikely, and some experiments by Spencer in which another species of Drosophila was reared on a food culture mixed with ground carnotite yielded no mutations. The cause of natural mutations is therefore much in doubt.

Types of Changes Artificially Produced.—The changes produced by the several kinds of radiation have been termed mutations, and it will naturally be assumed that changes in individual genes are meant. Since in the fore part of this chapter chromosome aberrations—change in number, inversions, translocations, deletions, etc.—are included among the primary evolutionary changes, it may be thought that the causes of these grosser alterations have been neglected. This is not true, however. Mutations have been emphasized in the foregoing account, but more radical changes were also effected in the radiation experiments. This is shown by their effects on crossing over, their lethal consequences, their bearing on linkage, or their influence on the behavior of other genes. Whole chromosomes have been abnormally distributed, and chromosomes have been fragmented by the treatment in all of the typical ways. It is therefore the general problem of primary change that is being attacked in the experiments described, not just the true mutations.

Cytoplasmic Mutations.—The possible causes of the small class of modifications arising in such cytoplasmic structures as the plastids have received little experimental attention. No artificial means of production of permanent changes in them has yet been discovered. Plants may be rendered yellowish by low temperature, by substances in the soil, or by bacterial or fungous parasites; but the effect disappears when the cause is removed. The form of chlorosis that causes variegation in many plants is of unknown origin. In some such plants the effects are infectious, but normal tissue must come into organic

contact with infected ones, as in a graft, to receive the infective agent. Examples of infectious variegation are one of the privets, an ornamental ash, and the Japanese burning bush. The thing transmitted is called a virus, which means chiefly that, while alive, it is not understood.

In unicellular animals which multiply by fission it has occasionally been possible to obtain unlike strains among the descendants of a single individual. Reproduction in these animals involves the whole organism; all of the material of the parent goes over into the offspring. This is in contrast with the higher animals and plants, in which a single cell out of millions on the female side, and little else than a nucleus on the male side, are transmitted. In these unicellular animals it is usually impossible to say whether divergence of the offspring of a single individual into two or more dissimilar strains is due to a change in the nuclear material (genes) or in the cytoplasm. When such changes occur frequently, but maintain themselves for a time, it may be suspected that the cytoplasm is being altered, or at least rearranged. In the protozoon Colpidium, Sonneborn has produced by different diets, within a single strain, lines that produced chain forms, and these have in turn produced individuals that gave rise to the original single type again. He regards the cytoplasm as being organized into units, and these as being rearranged in a manner comparable to translocations, inversions or duplications in chromosomes. Such changes must, of course, have little effect on the evolution of higher animals or plants, even if they should occur.

CHAPTER VIII

GENES AND CHARACTERS

> It is important to realize that the combination of several genes may give a result quite unlike the mere summation of their effects one at a time. This is obviously to be expected if genes act chemically. . . . To my mind it is probable that every gene produces a definite chemical effect, but we are very far from being able to prove this as yet.
>
> J. B. S. HALDANE, 1932.

When genes have been recombined or have mutated, when chromosomes have been increased or diminished in number or have had their parts misplaced or rearranged through deletions, inversions or translocations, they have made only the beginnings of evolution. These beginnings are for the most part false starts, for relatively few of the changes persist through many generations. The primary alterations initiated must also survive if species are to be modified by means of them. While survival is, as we shall see later, partly accidental, much of it is the outcome of a struggle with the environment.

In this struggle, it is not the genes themselves that are pitted against their surroundings. A gene survives if the individual in which it resides survives, and is lost if that individual perishes. A given type of gene becomes abundant if the individual organisms which possess it multiply rapidly, but declines in number if those individuals are of low fertility. In few cases do the genes owe their preservation or destruction *directly* to their own properties, and even in these few instances they fix their own destiny (usually destruction) by their effect (usually lethal, if any) upon the germ cells which contain them. Indirectly, however, they are masters of their own fate through their control of the characteristics of the organism. These qualities determine in large measure the success or failure of the individual, and hence the fortunes of the contained genes. It is important, therefore, to know the general rules in accordance with which the genes produce the organism's characters. It

has already been pointed out that no gene ever does anything by itself; its activities are all coöperative. Also, probably no gene has just one effect; it is involved in a variety of results. The things it is desirable to say concerning the relation of genes to characters and their influence on evolution are mostly elaborations, with particulars, of these two statements.

Dominance.—One of the simplest of the important features of gene control of characters is the relation between or among the genes occupying the same locus in homologous chromosomes. In most organisms there are two such genes at a given locus in each cell, but occasionally four or only one, and rarely, as a result of irregularities, other numbers. Attention may be confined largely to the situation in which there is a pair of genes of each kind.

When these two genes are alike no particular evolutionary problem is raised. When they are different, what character do they help produce? If in the latter case one of the genes is of a kind that is so widespread as to be properly regarded as the wild-type gene for its locus, while the other is less common and is presumably the result of a mutation from the wild-type gene, the character which develops in response to these genes (coöperating with other genes, of course) is usually nearly or quite identical with that which would develop if both genes were of the wild type. That is, one wild-type gene, even in the presence of a mutant gene at the same locus in the other homologous chromosome, has about the same effect as two wild-type genes have. The mutant gene can bring its alternative character to expression only if it is in both of the chromosomes, to the exclusion of the wild-type gene. These facts are expressed by saying that the wild-type gene is dominant, the mutant gene recessive.

The same relation between homologous genes exists in many domestic animals and cultivated plants whose genes can not be accurately designated as wild-type or mutant. When a fowl has a gene for rose comb (inaccurately so called, since other genes help in a minor way to produce the comb) in one chromosome, and a gene for single comb in the homologous chromosome, its comb is of the rose type, just as it would be if two rose genes were present. Rose comb is dominant. Single comb, which is produced only when two single-comb genes are present, is said to be recessive.

Sometimes one of the genes is not quite dominant over its mate, as in the black chaff of a certain variety of oats. A heterozygous plant has chaff a little less black than its black parent. In other instances, a heterozygous organism is distinctly intermediate between the two corresponding homozygotes in appearance. Thus, roan cattle are hybrids between red and white, or between black and white; pink four-o'clocks are heterozygous

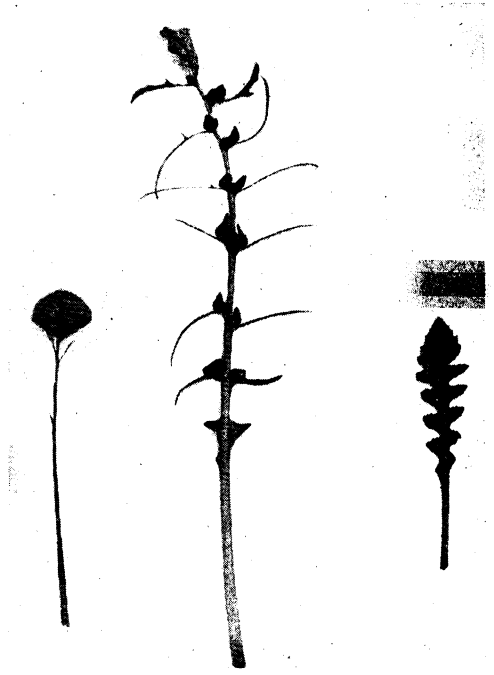


FIG. 37.—Leaf of rosette of hybrid shepherd's purse shown between its parent types. Despite the large size of the hybrid, which is due to hybrid vigor, its intermediacy in form between the parents is obvious. (*Photograph by Professor G. H. Shull.*)

for red and white; hemp seeds heterozygous for light and dark color are of an intermediate shade; and similar intermediacy is shown by the form of certain hybrid shepherd's-purse plants (Fig. 37). In all these readily distinguishable heterozygotes, neither gene is dominant over the other. This lack of dominance is the general rule, in Drosophila at least, when the two genes are both mutants from the wild type. Thus, of the 13 genes mentioned on page 79 as concerned with eve color and

all occupying the same locus, one is the wild-type gene, the rest all mutants from it. When a fly contains the mutant apricot gene and the mutant white gene, its eyes are pale apricot. Other pairs of mutant genes likewise usually produce an intermediate result.

With precise means of measuring or otherwise judging heterozygotes, it would probably be found that complete dominance of one gene over its mate is uncommon. Approximate dominance is, however, more frequent than the clear lack of it.

One noteworthy fact is that most mutant characters that have arisen under observation in recent years are almost completely recessive to the normal or wild-type characters of the species. A few so-called dominant mutations have occurred in Drosophila, such as curly wing and star eye. However, since flies that are homozygous for these dominant mutant genes are incapable of living, it is not really known whether they are dominant or not; and because of the inviability of the homozygotes, it has been suggested that some of these changes may not be gene mutations, but small deletions—that is, gaps in the chromosome.

Dominance is not an absolute quality of a given gene, but may differ in different situations. Agouti or gray coat in mice is dominant over nonagouti, but is recessive to yellow. Sometimes a gene is recessive when accompanied by one set of other genes, but dominant or at least partially so in the presence of another group of genes. Thus, forked bristle in Drosophila is regularly recessive, but with the introduction of a certain modifying gene the wild type is no longer dominant over it and the heterozygote is intermediate. Purple stem color in the Jimson weed Datura is dominant over green out of doors in summer; but in the greenhouse in winter the heterozygotes are intermediate between purple and green. Horns in certain breeds of sheep are dominant in the male, but recessive in the female. Dominance is thus a variable phenomenon.

Consequences of Dominance and Recessiveness.—An important evolutionary consequence of recessiveness is that genes may exist in individuals that give no sign of harboring them. When a gene mutates, its new form is usually recessive. Since the individual which contains it must usually have also a wild-type gene—that is, it is heterozygous—the new character does not show. This character might be unfavorable, or even lethal,

but the individual would suffer no damage from it. This is a very important element in the establishment of new genes, to be discussed in a later chapter.

Another result of recessiveness is the phenomenon of reversion. A recessive character can appear only in an individual both of whose genes at the pertinent locus are recessive. The recessive gene may be carried along in heterozygotes through a long series of generations, never coming to light because each heterozygote happens to mate with an individual homozygous for the dominant gene. When, however, two heterozygotes mate, there is one chance in four among their offspring for the recessive character to be expressed.

When more than two chromosomes (and hence genes) of a general kind exist in the cells of an organism, the dominance relation is variable. In one species of shepherd's purse, already mentioned on page 90, which has arisen by a doubling of the chromosome number, there are as a consequence four genes of a kind. At one locus there are in the species four genes for the shape of the seed capsule, and each gene may be either a dominant gene for triangular capsule, or a recessive one for spindle-shaped capsule. The four genes of any one plant may be any combination of the triangular and spindle-shaped genes. If even one of the four is the dominant gene, the seed capsule is triangular. That is, one dominant gene is dominant over three recessive ones. The only way to get a spindle-shaped capsule is to have all four of these genes recessive. However, in the endosperm of a corn grain, a tissue containing three genes at each locus, it is found in the contrast of flinty with floury that two genes of either kind are dominant over one of the other kind.

Coöperation among Genes.—When genes at different loci in the chromosomes are concerned, coöperation in the production of characters is the general, probably the universal, rule. Some instances of combined action are quite simple. If in the wild-type vinegar fly, which has red eyes, one pair of genes be changed by mutation in a certain manner, the eye becomes of a deep wine color called by geneticists claret. It is common practice, though only as a convenience, to call the modified genes the genes for claret eye, as if they alone were responsible. That they do not bear the whole burden of the eye color will be clear in a moment. If another pair of genes of a wild-type fly be

changed in a particular way, the eye color becomes scarlet, and the new genes are spoken of as those for scarlet eye. If, now, these two new pairs of genes be brought together in the same fly by hybridization, that fly has neither of the new eye colors, nor has it the wild-type red; its eyes are instead orange in color. The two genes are coöperating in the production of the eye pigment. It is obvious that calling one of the new factors the claret gene, the other the scarlet gene, results from the mere accident that the respective mutations were first detected in the progeny of wild-type flies. Thus, if the so-called claret gene had arisen in a stock which was already homozygous for scarlet

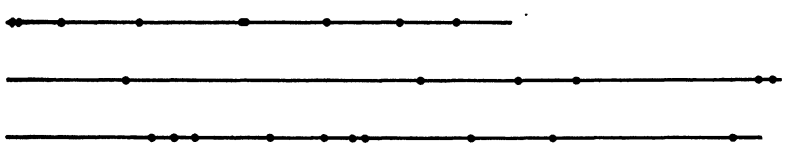


FIG. 38.—Diagram of the chromosomes of Drosophila showing the loci of 25 genes affecting eye color.

eyes, or better yet if the wild-type flies had had scarlet eyes, the claret mutant would have been recognized by its orange eyes, and the claret gene would have been called the orange gene. Similarly, if the wild flies had possessed claret eyes, the mutation which is now called scarlet would have been named orange.

Coöperation among genes in the production of visible characters occurs on a large scale. The interaction between the scarlet and claret genes introduces a much more extensive coöperation in the production of the red color of the wild-type Drosophila. Among the hundreds of genes of the wild-type fly that have mutated under observation, 25 have concerned eye color (Fig. 38). It follows that, in order to have red eyes, these 25 genes must remain unaltered. Change one pair of them, and the eye color is something different. Change another pair, alone, and a third color appears. Change two pairs of genes, and still a different color results. In no other animal has such extensive coöperation among genes in the production of one visible result been discovered, but this is presumably due only to the fact that no other animal is genetically so well known. That interaction is common is indicated by the considerable number of

instances of it known in various animals and plants. It occurs in the development of the walnut comb in fowls, several colors in mice, the gray coat of rodents in general, red color in pigs, purple color in sweet peas, the green color and some other colors of corn plants, the purple color of corn grains, flower color in snapdragons, red color in grains of wheat, spotted pattern in mice and beans, and many others.

So many of these interactions among genes are known, and the principle of interaction is in such close accord with what is known of the physiology of development, that they are probably to be regarded as universal. That is, no character is determined by a single pair of genes; and this statement means, not merely that a pair of genes would be incapable of producing anything in the absence of other genes, but that its product differs according to what other genes occur in the same individual.

Special Forms of Gene Interaction.—The influence of gene upon gene takes various forms. The color of White Leghorn fowls is due to a gene that suppresses all pigment production by other genes. Genes that would produce color are present, and give rise to Leghorn fowls of other colors when the inhibiting gene is absent. This inhibitor in the White Leghorn may be introduced by crosses into other breeds, but in them is not quite dominant, since flecks of color appear in the hybrids.

Sometimes a character is controlled by a number of genes of like nature having a cumulative effect. Each gene does the same thing as the others do, though not necessarily the same amount, and their effects are added. Size characters and the number of repeated parts are apt to be dependent on such multiple genes. Size of fruit in tomatoes, number of rows of grains on the ears of corn, length of ears in rabbits, length of tail and feet in certain mice, and red color of grain in wheat are among the characters determined by multiple genes. Blending inheritance is the ordinary result of multiple-gene determination. In this type of inheritance the hybrids of two distinctly unlike parents are intermediate between them but fairly uniform if the parents are homozygous, while the offspring of the interbred hybrids are variable, owing to the numerous different combinations of the genes.

When genes coöperate but have very unequal effects, some of them may be regarded as modifying genes. For example, spot-

ting in mice may be made to appear by the presence of just one certain pair of recessive genes in combination with almost any other genes. Nevertheless, the spots are of very different extent in different animals. These differences are due to the modifying genes, which have no visible effect at all in the absence of the spotting gene, but which in the presence of the latter govern the amount of spotting. Modifying genes appear to be common. An important consequence of them is that a character called by a certain name is not everywhere alike. It occurs differently in different individuals.

Multiple Effects of One Gene.—The fallacy of calling a gene the gene for blue eye, or the gene for spread wings, has already been pointed out, the basis of the objection to this designation being that many genes coöperate to achieve a joint result. The scheme of gene operations is much more complicated, however, than even this statement indicates. For, instead of coöperating merely for the production of one character, a gene frequently, perhaps always, takes part in the production of several or many characters. Thus, the gene for the dichaete character of Drosophila, so named because of the reduction of the thoracic bristles, also helps to effect a divergence of the wings which is much more noticeable than the bristle character. The gene for bent wing affects several characters besides the wing, but what these other characters are depends on the temperature. At moderate temperatures the legs are shortened and distorted; at low temperature the eyes are speckled, the wing veins broken, and the thoracic bristles disarranged. Club wing carries with it modification of certain bristles. The gene for white eye also modifies certain parts of the reproductive system. Spines and their absence on the seed capsules of the Jimson weed are due to a pair of genes which also change the thickness of the stems, the length of the internodes, and the habit of growth of the plant. In naming a gene, therefore, one selects only one of its effects, usually the one most easily ascertained, to suggest its designation.

The multiple effects referred to above are all structural. The responsible genes must, however, have physiological effects, since structure is attained only as a result of physiological processes acting during growth. It is not surprising, therefore, that among the numerous products of genes are physiological

qualities having no structural identification tag. In Drosophila most of the mutations which have arisen in laboratory cultures and are recognized by some structural modification have also a deleterious effect on fertility, viability and length of life. Flies exhibiting these mutations generally live a shorter time, and lay fewer eggs, and a smaller proportion of the eggs complete their development. The gene which constitutes the only difference between a yellow mouse and the wild-type agouti is fatal when present twice in the same individual. Since physiological qualities are not as a rule easily ascertained, the discovery of a few of them among the multiple effects of genes leads to the plausible assumption that there are many of them. As has been stated in the preceding chapter, these physiological properties must be far more important for the species than their structural features.

Environmental Effects.—Genes often have their actions modified by the environment. The effect of greenhouse and outdoor conditions on dominance of color in Datura, and of sex hormones on dominance of horns in sheep, have already been mentioned (page 112). There are many other environmental effects. Undernourishment, as is well known, commonly reduces the size of an organism; there are genes for growth, but environment may either help or counteract them. The vestigial wing of Drosophila responds remarkably to temperature, so that if kept warm enough during development it is practically identical with the normal wing. Varieties of wheat that are hard in some regions are soft in others, and the difference appears to be due to the time in development at which the nitrogenous foods of the plant become available. A giant tobacco variety goes on growing indefinitely, without flowering, if raised out of doors under ordinary conditions; but when brought indoors and reared under artificial light in shortened periods, it blooms seasonally like other varieties. Light is necessary to the development of green color in plants, as also are iron compounds; yet green color is inherited, as is shown by the existence of colorless varieties. One variety of corn has red seedcoats only if these are exposed to sunlight, colorless coats if kept in darkness.

In each of these cases there are genes that govern the characters in question; but their control is far from complete. Particularly significant are those instances in which an environ-

mental agent imitates the action of some of the genes. Thus, in corn there are varieties having red seed-coats whether the grains develop in light or in darkness; in the sunred variety just mentioned a certain gene and sunlight are both required to produce the red color.

The extent of environmental action is very variable. Some genes show practically no response to differences in the environment, at least to any conditions that commonly occur. Others exhibit great variability in their reactions. Only empirical tests can determine the stability or plasticity of the processes governed by any given gene. This susceptibility to environment, depending on various conditions, may be either an advantage or a disadvantage.

Genes Not Discoverable from Characters.—It must be clear from several of the preceding sections that the totality of the genes which an organism possesses cannot, as a rule, be ascertained by a mere inspection of its visible qualities. The interaction of genes to produce characters whose nature is not suspected until they are synthesized or analyzed; the existence of dominance which conceals the presence of certain genes; the modifying effects of the environment—all these contribute to the deception practiced by external appearance with respect to the genes within. Inhibiting genes are particularly deceptive. In poultry, as already stated, and in corn there are white varieties due to genes which suppress the action of any pigment-producing factors. This whiteness is indistinguishable from the whiteness due to the lack of pigment genes. A male butterfly of a certain species may possess a gene for white color, and still be yellow. This is not due to recessiveness of the white gene, for he may be homozygous for it, and yet be yellow. In the female this white gene is dominant, but something in the physiology of the male suppresses it completely. Another cause of concealment of the gene content is the physical masking of one character by another. Thus, black pigment in the hair of a mammal may obscure a yellow or red pigment, and heavy brown pigment on the front surface of the iris of the human eye hides the blue substance in the posterior portion.

An important evolutionary consequence of this lack of correspondence between the characteristics of an animal or plant and its genes is that whatever relation exists between the organ

ism and its environment need not exist between many of its descendants and the environment, even though the environment be wholly unchanged.

Fertility and Sterility.—One of the most important things a gene can do is to influence reproduction in such a way as to increase or diminish the number of descendants. Sometimes fertility is merely one phase of general activity, but not always. A capacity for reproduction below that of the general average is not infrequently sharply defined in the absence of any other marked physiological deficiency. An organism may be in most respects quite healthy and vigorous, and yet leave few descendants. This relative sterility has been extensively studied. Sometimes the object of this study is an inability to reproduce abundantly under any set of conditions. More often it is an incapacity in relation to certain systems of mating—sterility in self-fertilization, sterility in cross-fertilization, or sterility in crosses with particular types of individuals. In all these forms, the quality is of importance in evolution. Sometimes sterility is due to the possession of certain genes, a number of which have been demonstrated by experiment.

In plants the best known source of sterility lies in the slow growth of the pollen tube down the style. The pollen tube (Fig. 39) contains the male nuclei, and unless it reaches the ovules before the flower withers, fertilization does not take place. When pollen from two or more sources falls upon the same stigma, there is a race among their pollen tubes, and the swiftest growing kind performs the fertilization. The responsibility for swiftness rests not alone upon the pollen, but also with the tissues of the style, for growth of the pollen tube depends upon a reaction between the two. In some instances the reaction between pollen and style of the same flower, or of other flowers on the same plant, is so slow that no fertilization takes place, and self-sterility results. East has found this condition in several of the Nicotianas. Such self-sterile plants are readily fertilizable by pollen from other plants.

Plants are not always less responsive to their own pollen, for instances of reversal of this condition have been found. When their own pollen is mixed with foreign pollen, and the two are sprinkled on the stigmata, the plant's own pollen tubes frequently arrive first at the ovules. This is shown by choosing

foreign pollen from a plant possessing some different characteristic recognizable in the seed, so that the number of fertilizations by the two kinds of pollen may be ascertained by counting the two kinds of seeds. Jones has found that self-pollination thus predominates in corn, and similar results have been obtained in several other plants.

Sterility in particular crosses may result from the possession, by the organisms crossed, of dominant interacting genes. Each organism in such an instance possesses a gene which is harmless

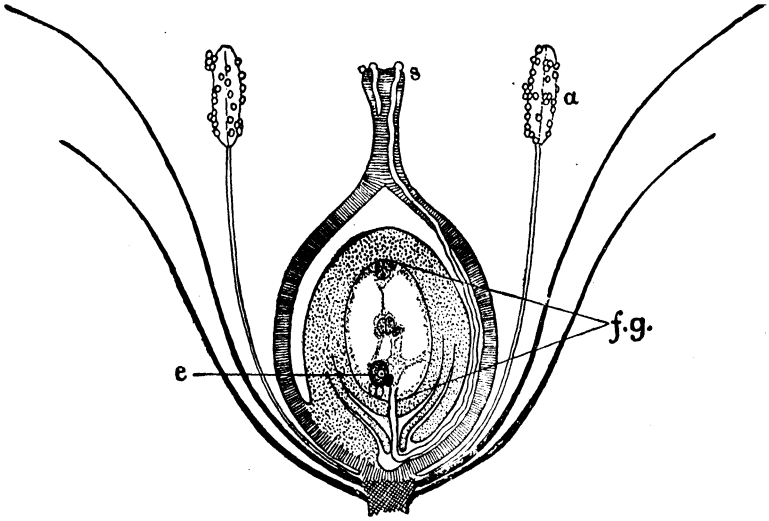


FIG. 39.—Pollen tubes growing through the style of a flower; *a*, anther bearing pollen; *e*, egg; *s*, stigma, upper end of style; *f.g.*, embryo sac. (*From Sinnott and Dunn, Principles of Genetics, McGraw-Hill.*)

by itself, but which when it gets into the same individual with the pertinent gene of the other organism, as it would in their hybrid, causes that hybrid to have diminished powers of reproduction or none at all. The genes have to be dominant in order that each one may produce its effect when it is present only once, as it is in the hybrid. Intersterility, as this relation between types may be called, is particularly important in the separation of species, and is discussed in that connection in Chap. XIV.

Sex-linked and Secondary Sexual Characters.—The relation of sex to X and Z chromosomes has been described. One sex has two of these chromosomes, the other only one. This distinction is responsible for a difference in the production of

certain characters in the two sexes. The genes of the X chromosomes in a male fly or mammal, for example, in which there is only one X, always come to expression whether they are recessive or dominant. The reason for this is that there is no other X chromosome in which there might be dominant concealing genes at the same loci. In the sex with two of these chromosomes, both genes of any pair must be recessive in order that the recessive character may develop. Characters dependent on genes in the X or Z chromosomes are said to be sex-linked. Certain evolutionary situations owe their nature to this difference between the sexes.

The other chief difference in the heredity of the two sexes relates to their secondary sexual characters. These are characters which are different in the two sexes but have nothing to do directly with reproduction. Tail feathers, combs, wattles and spurs in fowls, beard and baritone voice in man, the mane of the lion, and the brilliant colors of many male birds are examples. These characters are determined by genes, but animals of different kinds differ in the mechanism through which these genes express themselves in development. In the vertebrate animals, substances known as hormones are produced by the primary sex organs (ovaries, testes), and these hormones cause the secondary characters to develop. If through removal of these primary organs, or by any other means, an animal is deprived of its proper hormones the normal secondary characters do not develop. In insects, these special hormones appear to be lacking, and the secondary characters (color patterns, antennae) are produced more directly by the gene complex that determines sex. Extirpation or transplantation of the ovaries or testes has, in insects, no influence on the secondary characters.

CHAPTER IX

DIRECTION OF MUTATION

> Natural selection can only act on the variations available, and these are not, as Darwin thought, in every direction.
>
> J. B. S. HALDANE, 1932.

It has been shown in the foregoing part of this book that many observed phenomena of very different kinds can be satisfactorily explained only by assuming that evolution has occurred; that there is a mechanism in living things through which evolutionary changes may be brought about; and that a beginning has been made in the discovery of the agents which cause those changes. One important feature of evolution in nature, however, has been left entirely out of consideration. Nothing has been related which would indicate how the processes of change have arrived at the particular end result in the midst of which we find ourselves. Why evolution has resulted in the particular species, genera and higher groups now in existence; why so many forms were produced and lost by the wayside in past geological ages; and why so many imaginable types of living things have apparently never sprung up—these are important questions upon which the facts already given do not bear. The question of the direction which evolution has taken is, or at least may be, entirely independent of the questions whether, and why, it occurred. This question of guidance of the process of modification it is now necessary to consider at some length, in several successive chapters.

If mutations are the material of evolution, as geneticists are convinced they are, it is obvious that evolution may be directed in two general ways: (1) by the occurrence of mutations of certain types, not of others, and (2) by the differential survival of these mutations or their differential spread through the population. The former is the primary question, in the sense that it precedes the latter. Which is the more important of the two depends on the answer to the question what types of muta-

tions occur. It is with the determination of the types of mutations that the present chapter deals.

Is Mutation Random?—The statement is commonly made, even in biological circles though not usually among geneticists, that mutations occur fortuitously. While this assertion is sometimes intended to mean that the nature of mutations is in no way related to the environmental conditions in which they arise, it is usually meant to signify that the kind of mutation which occurs has no causal relation whatever. It has frequently been objected by those who opposed mutation as the means of evolution, that mutations are accidental. The implication which this objection was intended to convey was that evolution brought about by these aimless and ungoverned changes would end in chaos. R. A. Fisher (1930) has assumed that mutation occurs in every conceivable direction; and some of the most important of his conclusions regarding the outcome of natural selection, and the degree of adaptation of a species at any moment, depend upon the correctness of that assumption.

There are many things, however, which indicate that in the dealing out of mutations the cards are stacked. The available evidence goes to show that there are numerous restrictions upon the process of modification, so that the wheel of change, like the wheel of fortune in a well-managed casino, betrays a strong tendency to stop at certain points. To assume, under these circumstances, that every conceivable type of mutation not only may but will occur is like supposing that a tetrahedron will rest stably in twenty, or a hundred, or indefinitely numerous positions. Moreover, a casual glance at the mutations which have occurred abundantly in certain organisms suggests that they are limited in their nature. For example, the eye color of the fly Drosophila has mutated many times. Were the direction of these mutations subject to no control, all colors of the spectrum should be equally likely to occur. While many shades of red have resulted from these modifications, there has been no blue or green (Fig. 40). In view of the frequency of mutation of eye color, one is led to suspect that blues and greens are absent because Drosophila is incapable of mutating in that way.

Prominent among the other considerations which lead to the conclusion that mutation is not random is the chemical constitution of the genes. Mutation is in all probability a chemical

change of some sort. While the chemical composition of the genes is not known, this fact does not greatly affect the conclusion that changes in their constitution must, if they occur at all, be limited to a certain group. Even inorganic compounds are thus restricted; they enter into certain reactions readily, others with difficulty or not at all. If the genes are protein bodies, as is quite likely, they must share the great specificity which proteins in general possess. Indeed, the very action of slightly different gene complexes in producing minutely different structures, often at the very end of development, is an indication that such high specificity must exist. Even if the genes be enzymes, or any

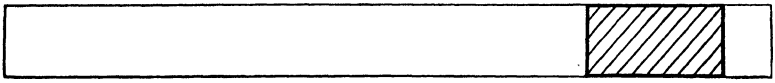


FIG. 40.—The nonrandom nature of eye-color mutations in Drosophila, shown by the small fraction of the visible spectrum (shaded) within which all such mutations have occurred.

other sort of chemical entity, they can hardly escape the limitations put upon their changes by their own composition.

Repeated Occurrence of Certain Mutations.—A further indication that the sort of change which genes undergo is not purely a matter of chance is found in the frequency with which some mutations recur. The number of mutations which might conceivably occur in an organism having two thousand genes is almost unlimited. In Drosophila something like 1000 of these possibilities have been realized. This is an insignificant fraction of the imaginable kinds; and yet, certain of the mutations have occurred again and again. A certain gene concerned with eye color has had much more than its share; probably forty changes in it have been observed, not including those artificially produced by X-ray treatment. More of these mutations have resulted in white eyes than in anything else, though there have been 11 other colors. Cut wing, rudimentary wing, vermilion eye and yellow body have occurred 15 or more times. More than 30 other mutations have occurred two or more times in Drosophila. Among them are forked bristles, lozenge eye, miniature wing, ruby eye, purple eye, ebony body color, pink eye, sepia eye, bent wing, and eyelessness. Every chromosome of Drosophila has contributed two or more identical mutations of

certain of its genes. In another species of Drosophila, *D. virilis*, a certain miniature-winged type mutates to the normal wild type with great frequency, amounting to more than 5 per cent in each generation. The snapdragon Antirrhinum has mutated to a curly-leaf type some 39 times, and many of the other mutations known in this plant have occurred twice independently. In corn also Stadler found occasional or frequent recurrence of certain mutations of the eight genes he studied. Were the direction of mutation wholly fortuitous such repetitions should be rare, and in view of the very limited numbers of mutations discovered would probably not have been found so far in any instance.

To the repetitions that have occurred in "natural" mutations must be added quite a few that have been induced artificially. In Muller's X-ray experiments, along with a number of mutations never before observed were several which had originated before. In the temperature experiments of Jollos, the commonest mutations were black and sooty body colors and abnormal abdomen, with all of which geneticists had long been familiar. Some of the somatic mutations, those affecting only body cells, belong in this category of repetitions, and are especially valuable because in their origin they show without further test that they are repetitions. Thus Patterson has, by X rays, caused some of the facets of the eye of Drosophila to be white. The white areas were of different sizes, depending on how early in development the mutation occurred. Now, white eye is a sex-linked character, which means that the gene differentiating it from red eye is in the X chromosome. The male fly has only one of these, and the white patches were occasionally induced in their eyes. The female, which has two X chromosomes, did not respond to the X-ray treatment because, to show the white areas, two mutations would have to occur at the same locus simultaneously, one in each chromosome of this pair in some cell. However, by employing female flies heterozygous for white eye, the white regions were produced about as freely as in the males. This could only happen by converting the normal red-eye gene of the one chromosome into the white by mutation. White areas could occur only if the induced mutation were identical with the white-eye gene already present in one of the chromosomes. That is, these white areas in females were all

due to repetitions of an old well-known mutation. In corn Emerson has found it easier to demonstrate somatic mutation in the endosperm color of the seeds, easier because the change was from recessive to dominant and came to expression immediately. In a recessive white or yellow grain, for example, the color gene mutated back to the dominant wild type (red, for example), producing a colored patch. These mutations occurred repeatedly, causing variegation of the seeds.

In all these cases, as pointed out above, the repeated occurrence of certain mutations affords evidence that mutation is not random but tends strongly to take place in certain set ways.

Parallel Mutation.—This conclusion that the direction of mutation is at least partly determined by the nature of the genes in which it occurs is rendered still more secure when identical mutations are produced in different lines of descent. This has happened in a small way in Drosophila, in strains obtained in different regions and presumably not closely related to one another, but in which the same mutations have arisen. Likewise, in the work of Jollos, in each of three stocks originating in widely separated collections of wild flies, the three mutations to black, ebony and abnormal abdomen were the prevailing changes.

Still more striking are the identical mutations that occur in different, but similar, species. The best example of this phenomenon is a pair of species of Drosophila, the classical *D. melanogaster* and its very apt imitator, *D. simulans*. These two species are so nearly alike in appearance that for a long time they were regarded as the same. When it was discovered that hybrids produced by crossing them were sterile, they were closely examined and several small differences detected. It is fortunate that hybrids, even sterile ones, can be produced, for it can thus be told whether mutations of the two species are alike. If a ruby-eyed *melanogaster* is mated with a ruby-eyed *simulans*, and ruby-eyed offspring are obtained, it is certain that ruby eye is the same thing in both species, for this character is recessive to normal eye color in both species. If the hybrid were of wild-type eye color, it would be known that the two ruby genes were not alike. Using this method, Sturtevant has shown that yellow body, prune, ruby and garnet eye colors, crossveinless, dusky, vesiculated and rudimentary wings, forked bristles, fused wing veins, and bobbed bristles, all sex-linked,

are identical in the two species. In two of the other pairs of chromosomes likewise identical genes occur.

Among the mammals somewhat similar, though not extensive, comparisons have been made between the guinea pig and the Peruvian cavy. While some of the characters used in this cross were not *observed* to arise as mutations in the two species, that origin is the simplest one that may be assumed. At any rate, the correspondence of several varietal characters in the two species is shown to be complete; that is, the genes involved are the same. In plants, the snapdragon has furnished results that are probably to be interpreted in the same way.

When groups of organisms so distantly related, or possessing such different chromosome numbers or incompatible genes, that they cannot be crossed, exhibit similar mutations, or varietal differences that presumably arose as mutations, it is not possible to prove directly that the genes responsible for the mutant characters are alike in the several groups. However, the existence of such similar characters strongly suggests that the mutations must have been very similar, if not identical. Thus, among the rodents, ruby eyes in combination with dilute fur color has occurred in all four of the principal laboratory members of this group—mice, rats, rabbits and guinea pigs. So also has recessive black hair color. A recessive yellow color is found in three of them, pink eyes and dilution in three, brown agouti in three, a dominant black color in two, whitish belly in two, Himalayan dilution (white fur with colored eyes) in two, and several others. Had mutation occurred in purely random directions, it is scarcely conceivable that all these similarities could exist. It seems necessary to assume that the kinds of mutation produced are determined by the inherent nature of the mutating genes, and that the mutations are alike in these similar groups because their genes are very much alike.

Reversibility of Mutation.—One feature of the problem of the direction of mutation which has received considerable attention is the question whether the change may be reversed. Long before the modern development of genetics, biologists had observed indications that evolution never retraced its steps. When a group of animals had undergone a series of modifications, it appeared never to return to its former condition. Paleontology afforded some of the most complete demonstrations of the

correctness of this generalization in the lines of evolution traced in an early chapter of this book. This rule, once arrived at, was applied to smaller changes. It was assumed that, in the fossil elephantlike animals, a lower jaw, having become long by evolutionary changes as in Trilophodon, could not become short again; Trilophodon was therefore considered an offshoot of the main line, which died out. When the molar teeth had changed from the tuberculate to the flat-topped grinding type, they could not return to the tuberculate form; hence Stegodon, with its grinding teeth, because it appeared while the tuberculate types were still abundant, was considered by many paleontologists as an offshoot, on the ground that otherwise its descendants must have reverted for a time to the tuberculate state before becoming finally grazers. The reasoning in this instance is not faultless, but it illustrates the conviction that evolution is irreversible. Anatomists adopted the same view, and many conclusions regarding the successive modifications in specific instances of evolution were influenced by that concept. The idea was applied to individual development, and it was held that, when undifferentiated cells were converted into specialized structures, they could not return to their former undifferentiated state. One portion of this conclusion was the rather important view that somatic cells, having become organized out of the simple cleavage products of an original germ cell, could not give rise to descendants which would revert to the simplicity of germ cells, a conclusion which had an important bearing on the supposed inheritance of acquired characters.

There is no necessity of deciding here whether these conclusions were valid. Most of them appeared to be in harmony with the observed facts. Whether the irreversibility of such changes involved any fundamental principle or not is, however, another question. When mutations began to be commonly discovered, the question of reversibility was transferred to them. Most mutant characters could be interpreted as the absence of something present in the original, and one school of geneticists came to regard the mutation process as being regularly the loss of something, either a gene or a part of a gene. Too little was (and is) known, of course, of the physiological processes by which a gene complex produces its characters to render it even probable that subtraction of a part from the adult organization could be

due only to elimination of something from the genes, but that assumption must tacitly have been made. If, therefore, a mutant gene could revert to the original condition, that fact would have an important bearing on the theory of mutation by loss. Geneticists were for this reason alert to discover any such reversals.

Such returns to the former condition have occurred in a number of genes. Thus, eosin eye of Drosophila originated as a mutation from white eye, and a later repetition of eosin came from the wild-type red. Now, from the eosin stocks have arisen both white and wild-type mutants, both returns to the original or reversals of the earlier mutation. In the X-ray experiments with Drosophila more mutations from the wild type to a recessive new gene have been obtained than from recessive to dominant

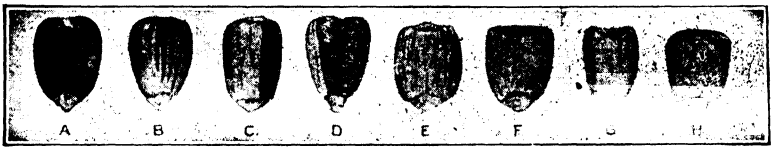


FIG. 41.—Variegation of corn, due to return mutation to a dominant color gene in the somatic cells. *A*, colored (dominant); *H*, colorless; *B–G*, variegations. (*From Emerson, in Genetics.*)

wild type, though this statement is not true of some stocks. In certain cultures which exhibited a recessive mutation, irradiation produced as many returns to the wild type as it had produced toward the mutant type in other stocks. The miniature-wing gene of *Drosophila virilis* mentioned earlier as mutating to wild type in 5 per cent of all individuals is, in all these cases, undergoing a return to a former state. In this species there are specific genes which, when present, greatly increase the rate at which this return mutation takes place.

Among the somatic mutations already mentioned as indicating that modification is directed from within are several return mutations. The variegation of grains of corn (Fig. 41), studied by Emerson, was due to mutation from a recessive colorless condition back to the original color in parts of the endosperm. Here again the frequency of these return mutations was increased by the presence of certain accessory genes. In the radiation experiments of Timoféeff-Ressovsky, in which somatic mutations were produced and detected in patches of different eye color,

one area was found to have mutated from eosin back to wild-type red. The occurrence of return mutations is thus well established both in the germ track and in somatic cells.

From the reversal of the direction of mutation in these cases may be drawn two important conclusions. The first, which is rather incidental to the main subject of this chapter, is that it shows that recessive mutations need not be losses; for, were they losses, return to the dominant original gene would seem to be precluded. Second, the reversal indicates that the direction of mutation is not purely fortuitous. Were later mutations of a gene which is itself the result of a mutation subject solely to chance for their direction, the great number of changes which the gene might conceivably undergo should make any one possibility, such as a return to the original gene, exceedingly rare. The fact that reversal is one of the commonest things which befall mutant genes, in case they mutate again, forbids the assumption that the direction of mutation is random.

Successive Mutations in One Direction.—In the early years of the discovery of mutations, when many biologists somehow felt that the direction of mutation might replace other guiding agencies of evolution, an important question was whether successive mutations in a given line of descent had any relation to one another with respect to their direction. The point at issue was the old doctrine of orthogenesis, literally evolution in a straight line, to be discussed in a later chapter (page 236). Numerous examples of successive steps in the same direction were provided by paleontology, such as the step-by-step reduction of the toes of the horse from four (or five) to one. It became a matter of speculation whether mutations might not succeed one another in orthogenetic series. Is the direction of a mutation in any way influenced by that of preceding mutations? More particularly, does one mutation of a given sort increase the probability that a further change of the same kind will take place later? Or is there anything in the nature of genes which should make their successive mutations progressive steps in any given direction? It is too early in this discussion to attempt to show whether successive mutations in the same direction might actually produce such orthogenetic changes as that in the horse's toes without aid from other forces. The question at present is merely whether successive mutations may be expected

to be, at least occasionally, cumulative steps in one direction by virtue of any principle other than chance.

Observation of mutations as they occurred naturally in Drosophila led to the conclusion that no such straight-line mutation was to be expected. This was indicated by the order in which multiple alleles, or different mutations of the same gene, took place. The best known and longest series of multiple alleles in the vinegar fly is that including coral, blood, cherry, eosin, buff, tinged, ecru, white and several other eye colors, besides the original wild-type red. These colors present different intensities of red, with white representing the extreme divergence from red. If the first of all these mutations had been that nearest the wild type, and if from this the next lighter one had originated by mutation, and this in turn had produced the next lighter, and so on with white appearing last, this series of alleles might have been regarded as an example of directed mutation. The actual order, however, was different, since white was the first, and the intermediate colors were distributed irregularly in time. Moreover, instead of one mutant giving rise to another, all these mutations came directly from the wild type except one, eosin, which arose first from white. There is no a priori reason to expect mutation to occur repeatedly in the same direction unless one holds that genes are in some way different quantities of the same thing, a view supported by Goldschmidt and some others. Even if alleles are thus quantitatively related to each other, it does not follow that each mutation must be the smallest unit change in that quantity. One mutation might consist of the entire possible change, the next one, starting from the original gene again, might be only half the possible modification, and so on. This is what must be supposed to have happened in the white series of eye colors in Drosophila, if the genes are quantities of something; but most geneticists are not of the opinion that allelic genes differ only in quantity, they regard them as different in quality.

One would draw from the above facts the conclusion that repeated mutations are not directed as a series. Apparently opposed to this conclusion are some experiments of Jollos (see also page 239) in which heat-produced mutations obtained in successive generations were said to constitute progressive changes. A dusky body color, for example, occurred early;

this was followed by a deeper black which he called very weak sooty, this by weak sooty, then sooty, then ebony—each darker than the one preceding it. The later members of this series were crossed with the well known mutants bearing the same name, and were found to be identical with them. The heat experiments have, however, been repeated by Plough and Ives who, while verifying the artificial production of the mutations, get no evidence of successive steps in the same direction. Little stress can therefore be placed on mutation as a source of directed change involving a series of stages.

Direction Not Related to Environment.—An important feature of mutation has always been that its direction seemed to have no relation to the environment. Of the hundreds of mutations that have been discovered in various plants and animals, not one has shown any indication that its *nature* was environmentally determined. Mutations might owe their occurrence to the environment, as was proved for some of them by the irradiation and heat experiments, and as may be true of all the rest; but never did their nature seem to be determined thus. The X-ray mutations were not of any particular sort which would indicate origin through radiations. The heat mutations, more often black, ebony and abnormal abdomen, did not by their nature suggest heat to have been the cause. In particular, mutations were never obviously adaptive; mutant organisms were not, so far as could be seen, better fitted for the environment than were the types from which they sprang.

In anticipation of a later discussion, it should be said that this nonadaptive feature of mutation is both a help and a hindrance when explanations of evolution are being sought. Adaptive characters of genera and families are not to be explained by means of nonadaptive mutations without invoking the aid of some other agent. But the nonadaptive distinctions between species may get their start in this manner.

Direction of Chromosomal Aberrations.—From the greater frequency with which chromosome numbers have been doubled, as compared with other types of chromosome aberrations, one might be inclined to conclude that something in the constitution of cells favors this mode of change, and that the aberration is thus directed. While it is not unlikely that doubling is an easier change than most other aberrations, the evidence for this

assumption is not so great as it at first appears. For the prevalence of $4n$ species, or higher multiples of some basic number, must be in large measure due to the greater viability of such combinations. More of them are known because more of them survive, and *perhaps* to a lesser degree because more of them arise.

The other chromosomal aberrations, such as translocation and inversion, probably owe their nature (though not their occurrence) purely to chance, though nothing is known which really bears upon this point.

CHAPTER X

SHIFTING GENE RATIOS

> The elementary evolutionary process in a Mendelian population is change of gene frequency. . . . What characterizes a species is a certain ratio of each series of allelomorphs.
>
> SEWALL WRIGHT, 1933, 1931.

To appreciate the extent to which evolution of species may be due to recombination of characters already in existence, it is necessary to recall the characteristics of species as outlined in the first chapter. Of particular importance in this connection are on the one hand the high degree of permanence of species, and on the other their plasticity or capacity to change. Species maintain themselves in much the same condition for many generations in succession, yet slow modification may creep in.

Stability, Plasticity and Genes.—The permanence of a species must be due to the possession by nearly all individuals in it of a large number of genes in common. Most members of the species are homozygous for most of these genes, consequently breed true. The origin of any gene held in common must in most cases have been one single original mutation which spread through the whole species. Most of the loci of chromosomes must be occupied by genes that are alike in almost all individuals of the species; on this likeness the existence of species depends.

In addition to the large number of genes held in common in the homozygous state by the great bulk of individuals, there is a smaller number of genes in which individuals differ. Each chromosome locus, in this smaller class, is the seat of at least two genes, one of which may usually be regarded as the wild type, the other a mutation from the wild type. Usually, though not always, the wild-type gene is dominant or nearly dominant over the mutant, so that heterozygotes exhibit the wild-type character. Often in observed instances a chromosome locus may be the seat of three or more genes, which are then known as multiple alleles, as indicated in the preceding chapter. These

multiple alleles have arisen by two or more different mutations of the wild-type gene, or by one mutation of the wild-type gene followed by one or more mutations of the mutant gene. It is probable that all genes are capable of mutating in more than one way, so that multiple alleles are common. Among multiple alleles the wild-type gene is pretty regularly dominant over each of the mutants, but the mutants lack dominance over one another, as stated on page 111.

Potential Variance at Any One Moment.—These genes which are different in the corresponding loci of the chromosomes of different individuals are the source of a considerable amount of variance in probably all species. This variance as it relates to a single locus occupied by only two different genes has already been touched upon on pages 83 and 84, where it is shown that the three types of individuals with respect to that locus are expected to be present in a given ratio. As a source of variety, however, these different genes are much more important than was there indicated, since many loci instead of just one, and more than two genes at one locus, are apt to be involved in any given population. If, for example, the members of a species were alike in all but ten of their pairs of genes; and if each of the ten wild-type genes had mutated only once so that two possibilities existed with respect to each of these ten loci; and if the wild-type gene be dominant over its mutant in each case, so that only two kinds of individuals might exist with respect to each of the ten pairs; then the individuals of the species might exist in 2^{10}, or 1024, different forms. Now, ten unfixed pairs of genes out of a total which in most species must run into the thousands, is a very small amount. On the average the amount of variance from this source must be many times that amount. For in any group of individuals which had mutated enough and multiplied enough to be recognized as a distinct species, even though a young one, mutation would have to have been sharply curtailed about the time of its arrival at the dignity of a species to have resulted in only ten further mutational types. No one knows the whole number of mutant genes possessed by any species, but in Drosophila some 1000 of them have arisen or been discovered in laboratory cultures, all within what is still regarded as a single species. This number makes the assumption of 50 or 100 mutations in a species appear highly conservative. If

only 50 loci are the seats of two different genes each, and dominance be assumed, then 2^{50} or more than a thousand million million kinds of individuals may exist. If any of the 50 genes had mutated more than once, yielding multiple alleles, or if dominance were sometimes lacking so that additional appearances resulted with respect to some of the genes, the number of kinds of individuals would be correspondingly greater. It is safe to assume, therefore, that most species are capable of an enormous amount of variability without any modification of the genes beyond that which already exists.

The linkage of genes, that is, their occurrence in the same chromosome with one another, does not in the least affect the above conclusion, as has been shown on page 81. Linkage may slow down the process of recombination, but once linkage is broken the new combination persists as tenaciously as the old, so that after a small number of generations there is no appreciable reduction in the number of individuals showing any particular composition.

Statistical Gene Concept of Species.—Under the circumstances just outlined, it is clear that the nature of any species is not defined by the very great majority of genes in which most individuals are alike. If any of the mutant genes are numerous enough to exist in individuals in the homozygous state (*aa*), and so influence the observable characteristics, the species is visibly altered in proportion to the number of individuals exhibiting the mutant characters. A species cannot be limited, in definition, to its universal characters, but must have sufficiently vague boundaries to include the occasionally outcropping types. Sometimes a mutant gene is so abundant as to determine the appearance of large numbers of individuals, with the result that a distinct variety exists.

Even when the mutant genes are so rare as never to influence the appearance of an individual, because found only in heterozygotes (*Aa*), their existence and abundance are potentially of great significance in the evolution of the species. To illustrate, assume that a recessive mutation has just occurred, and hence that the mutant gene exists in just one individual (*Aa*) among a million produced by ten thousand parents. Assume further that the biological situation is such that the species does not increase in numbers, hence that only ten thousand of the million

survive. The chance that the gene *a* will leap even this first hurdle is very small. If, however, the gene *a* exist in a thousand individuals instead of one, it may still be only in the heterozygous state and not help in the least to determine the visible form of the species; and yet, because it has a good chance to escape elimination, its prospect of sometime influencing the nature of the species is excellent. In other words, a population including only one *Aa* individual in a million, and a population with a thousand *Aa* individuals in a million, while looking alike, are very differently situated with respect to probable future evolution.

Both from the standpoint of appearance, and from that of evolutionary prospects, then, species must take on a statistical significance. They consist of such and such a proportion of gene *A*, so many *a;* a certain percentage of *B*, another of *b*, and another of *b'* (representing multiple alleles); and so on for all the loci of their chromosomes. A species which, over a number of generations, has markedly changed the proportion of some gene has undergone evolution, no matter how little its individuals may have changed in appearance. With this concept in mind, let us see what the possibilities of evolution are.

Stable Gene Ratio.—The proportion of the chromosomes of a species containing a certain gene at a given locus may be altered by unequal mortality or unequal fecundity of the individuals possessing the contrasted genes, by migration of such individuals into or out of the population, by unequal viability of the germ cells containing them, or by further mutation of the genes in that locus. In the absence of any such cause of change, the population should remain the same indefinitely, subject only to the vagaries of chance. There is nothing about the genes themselves, their dominance or recessiveness, and nothing in the mode of reproduction which should change their relative numbers. Starting with a given percentage of each gene of the unfixed group, a species should promptly arrive at an equilibrium of the genes which would thereafter be maintained except as purely accidentally altered. The situation has been simply illustrated (page 83) with a single locus, the wild-type gene (*A*) of which has mutated but once to the recessive gene *a*, so that only two genes for this locus exist in the species. Individuals of three kinds, *AA*, *Aa* and *aa*, are to be expected if cross-fertilization occurs, regardless of the way the contrasted

genes are combined in individuals at the outset. Suppose, as in the former discussion, that at any given moment the number of chromosomes containing *A* at this locus constitute a fraction p of all the chromosomes of this kind; that gene *a* be found in the fraction q of all the corresponding chromosomes; and that of course $p + q = 1$. If all individuals in an indefinitely large population, freely interbreeding, reproduce at the same rate, and all types survive to the same degree, and if there is no linkage and no overlapping of generations, the next generation will consist of p^2 individuals of the composition *AA*, 2pq individuals whose genes are *Aa*, and q^2 individuals that are *aa*. In the next generation, under the same stipulations regarding free intercrossing, random survival, etc., the three combinations should occur in the same ratio, and so on indefinitely. In each generation the two genes are still in the proportion of p*A* to q*a*. The ratio of genes is stable and remains so unless something happens to disturb it. Any one who does not trust the algebraic calculation necessary to arrive at this conclusion can readily substitute for p and q any specific values, such as 0.8 and 0.2 respectively, and demonstrate that with random combination they should retain these values generation after generation.

Accidental Variation of Gene Ratios.—Like all matters of chance, however, gene ratios seldom turn out just as expected. Either gene of a homologous pair may, as a result of random matings or random survival, be somewhat more abundant in one generation than in the preceding. A fraction expected to be 0.6 in any generation because that was the fraction in the preceding generation may easily be 0.65 instead. If that happens, there is no expectation of a return to the 0.6 in the following generation; the population should, as a matter of pure accident, stabilize at once at the new level, with the gene in question present in 0.65 of all the homologous chromosomes. After another accidental shift of this fraction, either up or down, stabilization should occur at the new level in the very next generation.

Actually, of course, the result is almost never exactly what it should be, just as almost never do 50 per cent of a handful of coins turn heads up when tossed. If a gene ratio should by accident shift in favor of a certain gene several generations in succession, considerable impetus to evolution might thereby be given. Such successive changes in one direction should be

rare; how rare would depend on the extent of the change in each generation and the number of successive changes in the same direction. Nevertheless, among many different genes, and many successive generations, there is opportunity for even rare events to occur; and less extensive changes covering fewer generations could be fairly common. Wright, who has made an extensive statistical study of the evolution problem, is of the opinion that important changes of gene ratios, particularly in the early stages of such changes, may and frequently do result from chance alone. Fisher likewise concludes that chance is the most important factor in the survival of a gene so long as there are only a few individuals that possess it. Wright also points out that the proportions of *AA*, *Aa* and *aa* individuals may change accidentally, so that one of the homozygotes may outstrip the other kinds, thus resulting in fixation of the gene and the loss of all variability with respect to it.

It should be noted that the random results described above are those expected for large populations. In small populations there is a tendency for the homozygous combinations to increase at the expense of the heterozygotes, resulting eventually in loss of the variance due to unfixed genes. The expected distribution of *AA*, *Aa* and *aa* individuals is based on uniform distribution of the genes. If a species is divided into subgroups, each having a different ratio, the homozygous classes again increase at the expense of the heterozygotes. Since subgroups may themselves form in a species range purely as the result of random changes of gene ratios, it is clear that random events may play a rather important role in evolution. Accident has often been claimed in the past to be of significance in evolution, and as often vehemently rejected; but only in recent years, in the work of Wright, Fisher and Haldane has it received such adequate statistical support and been assigned so definite a sphere.

Repeated Mutation an Aid in Establishing Genes.—When a mutation first occurs, the new gene exists in only one chromosome in each cell of one individual, which is thus heterozygous for it. If, as pointed out earlier in this chapter, the population is nearly constant in numbers, which usually means that many individuals in each generation are lost, the chance that this one individual and its new gene will survive is rather small. If it be assumed, as was done before, that the individual containing the

gene is one in a rising generation of a million, and that this number is reduced to ten thousand before maturity, and that the survivors are determined purely by chance, the probability that the mutation will be preserved is one in a hundred. If it escapes this elimination and mates, and the pair produces 200 offspring, equally with all other pairs, so as to yield again a million young individuals, one hundred of these individuals will contain the mutant gene. The situation of the new gene with respect to survival is now very much improved, since even with a 99 per cent reduction of the population before maturity it is likely to be included among the survivors.

Thus in its early history a gene leads a precarious existence. Its likelihood of becoming established may be increased by reducing the destruction, which would occur if the population were increasing in numbers. Its chance would be diminished if the population were decreasing in numbers, for this decrease would be accomplished by a rise in the mortality rate in each generation.

Probably the most effective aid in establishing new genes lies in their repeated production by independent mutations. A gene produced twice by mutation has twice as good a chance to survive as if produced only once. A gene that has only one chance in a hundred of surviving need be produced anew only fifty times to have an equal chance of success or failure. If a given mutation were to happen often enough, and nothing opposed its survival, it could easily spread through the entire species, replacing all other genes at the same locus. Indeed, that is precisely what it would be expected to do; for, with each mutation, the new gene's fraction of the whole population would be by just so much increased. Survival is assumed to be accidental, and eventually the survivors would possess only the new gene.

It is well known that certain mutations arise repeatedly. Some examples have been cited in the preceding chapter, where they were used as evidence that mutation is directed, not random. How widespread the repetition is, whether it occurs in the cases of all mutant genes or any considerable fraction of them, is unknown. So far as observations go, the known genes are very unequal in the frequency of their *de novo* origins. In Drosophila, white eye has arisen by mutation about a dozen times, a number of other genes a smaller number of times each. The bulk of

them, however, have been observed to appear only once; all the genes of these kinds now in existence in Drosophila cultures have descended from the "original" ones. Whether this great difference in the *recorded* frequency of appearance of the several mutations is a measure of the difference of the *actual* frequency, or whether some mutant characters are so much more easily recognized as to account for their more frequent discovery, must remain for the present in conjecture. White eye is not much more easily seen than yellow body, or sooty body, or rudimentary wing; hence it would seem probable that some genes mutate to a given new gene more often than others.

Nevertheless Fisher, and following him Ford, have concluded that nearly all the mutations now arising in organisms are old. Fisher is probably the more inclined to this view because of his concept of the origin of dominance and recessiveness. This concept need not be described; it may be said here, however, that the method of becoming recessive would necessitate in most instances the recurrence of the mutation a number of times. Neither Fisher nor Wright regards recurrence of mutations ("mutation pressure") as one of the major factors of evolution, but agree that in the early history of a gene it may spell the difference between elimination and establishment.

Migration and the Frequency of Genes.—When a gene arises, its frequency can be changed, aside from recurrent mutation, only by gain or loss of the individuals possessing it. When it has spread evenly through the entire range of the species, gain or loss of such individuals means preservation or destruction of them. Frequently, however, the pertinent frequency of a gene is not its frequency in the species as a whole, but in some restricted portion of the species. It has already been shown that random recombination may result in different gene ratios arising in different portions of a range, thus producing local races. Environmental differences may, as will be pointed out later, accentuate this differentiation. If it is one of these local races whose genes are under consideration, it is obvious that the frequency of a given gene may be reduced by the emigration of a disproportionate number of individuals possessing the gene out into the neighboring groups, and that its frequency may be increased by immigration of certain types of individuals from surrounding races.

Migration *tends* to render gene ratios everywhere the same. In so far as it succeeds it makes the entire species a unit by rendering its genetic composition approximately uniform. However, the migratory instinct of most animals is not sufficient to insure this homogeneity of the species. Aside from the spring and fall migrations of birds, the periodic pilgrimages of certain fishes, and a few other instances of extensive journeys, animals travel within surprisingly small limits. Trapping records designed to establish the phenomenon of "territory" have shown that a mouse may wander over an acre or two, in a single season of activity, or a bird fly only or chiefly within a radius of half a mile of its nest or some central point. Territory has been investigated in only a few groups, and it is not known how prevalent this limitation may be. Since, however, it must rest on some psychological basis it can hardly be expected in the very low forms of life. In these simpler groups the suitable environments are mostly in isolated patches, and this segregation suffices to prevent extensive intermingling. Wright estimates that, taking all factors into account, in a widespread species with many local races, the interchange of thousands of individuals between subgroups in each generation might easily be insufficient to insure general uniformity of the gene ratios. Varieties may thus spring up as a result of random drift of individuals possessing certain gene compositions. The distinguishing features of varieties established in this random way should not be adaptive, that is, not related in any favorable way to their respective regions. Since, as is pointed out in the first chapter, the observed differences between varieties of a species appear not to be adaptive, the idea that their origin is fortuitous and notwithstanding migration is still further supported.

When migration is very small, it can be shown statistically that there is a tendency for one or another of the genes of a given chromosome locus to become fixed, that is, to become established in a population to the exclusion of the other alleles. Heterogeneity, or the variance on which much evolution depends, is thus favored by a certain amount of wandering.

Not only in relation to genes already in existence does meagerness of migration tend to allow local races to form, but also in relation to origin of new genes by mutation. If a mutation occurs only once, and survives, and there is little migration

of the individuals possessing the mutant gene, there is bound to arise a local subgroup in which that gene is common. It may become common enough to be exhibited even if recessive, and so produce a visibly different variety. Only by frequent recurrence of the mutation, and its survival each time, in all parts of the species range, could the formation of a local race be prevented.

Useful and Harmful Genes and Their Survival.—In all the foregoing discussion, in order to isolate the factors under consideration, it was assumed that all genes at a given locus were equally capable of maintaining themselves. Nearly always, however, one or more genes are better adapted to the existing conditions than are their alleles. These favored genes are said to possess a selective advantage. They may help to secure for their possessors long life, freedom from disease, ease of mating, or high fertility, thus in some way causing the individuals containing them to leave more descendants. The advantage of a gene over its alleles may be very slight, and still enable it to prevail over them. Also, its disadvantage need be only very small to bring about its failure. The neutral range is very narrow—so narrow that Fisher concludes few genes can occupy it. In his opinion little of the evolution process would be missed if neutral genes were ignored. It is not easy to judge whether this opinion is correct, for there are ways by which even slightly harmful genes may survive for a longer or shorter time.

One means of survival of deleterious genes is found in their recessiveness, which is quite usual. If a gene is completely recessive, the character of a heterozygote is determined by the allelic gene. So long as the recessive gene exists only in heterozygotes, its fate is the same whether it is harmful, beneficial or neutral. Even when the gene becomes abundant enough to occur in homozygotes, and so produce the harmful character, there will always be a considerable number of heterozygotes also, unless the species is a regularly self-fertilizing one. Production of homozygotes will serve to reduce the frequency of the gene because these homozygotes will experience the lowered fecundity, decreased capacity for mating, or whatever handicap the gene imposes; but it can only reduce the gene to such numbers as will cause it to exist only in heterozygotes, for at that point its deleterious effect ends.

If a harmful gene is not wholly recessive, so that it influences the nature of heterozygotes, it will be subject at all times to the restrictive action of selection. The effect will be in proportion to its harmfulness and its lack of recessiveness. Such a gene, if its effect is appreciable, would have to be favored by an exceedingly unlikely succession of accidental survivals in order to maintain itself.

If a gene is dominant and harmful, it cannot last long, for every individual that possesses the gene even in one chromosome per cell shows the character. It is thus bred out of the population, with a speed dependent upon the degree to which it reduces the number of progeny.

It should be clear, after the above discussion, that if a mutation is a useful one it should be aided in the process of becoming established. This aid should not be very apparent at first, for if the new gene is recessive its advantage is of no avail until homozygotes arise. Even if dominant, the advantage may be such as to have no influence upon the survival of the original mutant individual. For example, if the elimination of excess individuals in each generation is determined mostly by chance, and if the advantage afforded by the new dominant gene is greater fecundity, the usefulness of the gene does not help at once. If, however, the dominant mutant individual survives the first accidental elimination, its higher fecundity insures it a greater proportionate representation in the next generation. Once it becomes established, the advantageous gene should then spread, rapidly or slowly in proportion to the increase of fertility which it entails.

It will thus be seen that the early, though perhaps not the immediate nor the ultimate, fate of a gene, be it useful or harmful, depends on whether it is recessive or dominant in relation to the wild-type gene from which it sprang. There are certain consequences of this fact, but since they are more closely related to the problem of the direction of evolution in general than to the mere shifting of gene ratios, they are postponed to the following chapter.

Combined Influence of All Factors.—It cannot be too strongly emphasized that the things that are eliminated from, or preserved in, populations are primarily not genes, but individuals. Whatever be the cause of an animal's death, or its failure to reproduce,

all that animal's genes are lost. If any genes of the same kinds are to survive, they must do so in other individuals. Accidental loss or preservation is the fate of whole organisms, and selective advantage or disadvantage is a property of whole organisms. Now, it is possible for one gene to be so supremely harmful that no combination of other genes can save the animal that possesses it, but that is not the usual situation. Likewise, it is *conceivable* that a single gene might be so signally advantageous that it would save an animal in spite of any harmful array of other genes, but it is unlikely that such a gene ever existed. In other words, harmful genes may be preserved under the protection of useful ones, and beneficial genes may be lost because of the bad company they keep. It is the totality of genes, usually a balance of plus against minus influences, that determines the capacity of a gene to survive at any particular time or place.

Gene ratios are thus dependent upon complexly interwoven circumstances. The other factors influencing them, recurrent mutation and migration, while not affecting the lives of individuals, may work in harmony, or oppose one another, in every possible combination. To arrive at the percentage of chromosomes containing a certain gene, many influences have been at work. In the preceding sections an attempt has been made to keep these factors apart. It is desirable to bring them together, but not an easy task. Mutation to a new gene is opposed by reverse mutation back to the wild type. Selection may favor heterozygous types against both homozygous forms. Repeated mutation may oppose (though usually ineffectively) the effect of selection. Migration may increase or diminish the results of other factors. If assumptions be made regarding the value of each of these influences, the evolutionary consequences of all in combination may be formulated. Wright has done this for a number of conceivable relations, and any one qualified by a mathematical training to follow his reasoning should consult his work. Others will have to be content with the foregoing brief statement, and that which follows. In general, any combination of values leads the population to an equilibrium at certain gene ratios.

Size of Population.—A surprising feature of Wright's calculations is the part played by size of population. Sharp reduction

of the population entails the fixation (homozygous condition) and loss of genes. In a small population inbreeding must be very common and quite close. In such a small group there is consequently little variance, and little chance for selection. Evolution in a small assemblage of interbreeding individuals must await the occasional production of mutations; and since these are usually deleterious and have an excellent chance of arriving quickly at the homozygous state and so exhibiting their effects, they tend to bring on degeneration and extinction of the group. A great increase of numbers in a population that has long been inbred leads to increased heterozygosis, partly dependent on new mutations, hence to new opportunities for recombination and changes in gene ratios. If a population is very large, all gene frequencies reach an equilibrium appropriate to the conditions prevailing, and there is little evolution. A change of conditions, altering the effects of selection, modifies all gene ratios which remain at the new level as long as the conditions continue. Evolution must be slow under these circumstances.

If both small populations and large ones are unfavorable to rapid evolution, the situation is very different in populations of intermediate size. In such medium assemblages there is opportunity for continuous random shifting of gene ratios. Intensity of selection changes as a consequence, being so low at times as to allow rather free play to random shift, at other times high enough to lead quickly to enhanced fitness to the environment. The speed of this change is of course fundamentally limited by the mutation rate, and even a "rapid" change may require, as Wright estimates, a hundred thousand generations for an important modification of the species.

The most favorable situation for rapid evolution, Wright concludes, lies in a large species divided into many local races, partially isolated and of small size. Random shift may occur within and between these races even without selective influence of varied environmental conditions. With such selection, the modification becomes more rapid. Such differentiation tends to continue without end, is not capable of reversal, and leads eventually to adaptive characteristics. Isolation of one group from the rest, by any means whatever, may lead to formation of a new species, differing from its neighbors mainly in useless

characters, but possessing the capacity of developing along adaptive lines as well.

Résumé.—A species is a statistical entity whose nature depends on the relative numbers of genes of those pairs which are not fixed and common to all individuals. Recombination and shifting of these gene ratios are capable of effecting an enormous amount of evolution even without further mutation. Gene ratios tend to remain stable, and the various types of individuals to reach an equilibrium, unless they are disturbed. Disturbance of the equilibrium may come about by purely accidental survival or elimination of individuals, by mutation to new genes and back to the original, by migration to and from the population, and by selective action of the favorable or unfavorable qualities of the genes themselves. These influences may be formulated if assumptions be made regarding their relative or absolute values. Both small size and large size of the population tend to restrict the opportunities for evolution, while intermediate populations are more favorable. The most favorable condition for evolution is that of a large species divided into many local races or varieties. These shifts of gene ratios lie at the foundation of all guidance of evolution.

CHAPTER XI

GUIDANCE BY NATURAL SELECTION

> As the field of existence is limited and preoccupied, it is only the hardier, more robust, better suited to circumstance individuals, who are able to struggle forward to maturity, these inhabiting only the situations to which they have superior adaptation and greater power of occupancy than any other kind; the weaker, less circumstance-suited, being prematurely destroyed.
>
> PATRICK MATTHEW, 1831.

One idea contained in the last chapter has enjoyed a much greater vogue in evolution theory than is there intimated. It is the idea that the prevalence of a given gene may be influenced by the usefulness or harmfulness of any character which it may help to produce. The prevalence of a gene can be increased or diminished only by raising or lowering the proportion of chromosomes, hence in the long run of individuals, possessing it. If the characters determined by the gene in question are such as aid the individual to succeed measurably better than other individuals lacking it, that gene should spread to a larger fraction of the population. Conversely, if the characters developing in response to this gene are such as to restrict certain fundamental activities of the individual as compared with individuals not possessing it, the gene must decrease in frequency.

The Natural Selection Idea as Developed by Darwin.—The role of advantage and disadvantage of characteristics in the guidance of evolution was recognized long before the genetic mechanism was understood. It was the theme of Charles Darwin's "Origin of Species" published in 1859, and was in Darwin's mind for the greater part of two decades before he put it into print. As conceived by Darwin (portrait Fig. 42), the shifting of characteristics of organisms in relation to their usefulness depended on the occurrence of a struggle for existence. He was impressed by the prodigality with which most living things produce offspring, the potential numbers ranging from

dozens to millions from each pair of parents. Should all of these offspring succeed and possess their parents' fertility, the numbers of individuals would increase in geometric ratio. Even for those species which produce only a few offspring, and in which the generations pass slowly, there would eventually be enormous increases in the population. Common observation

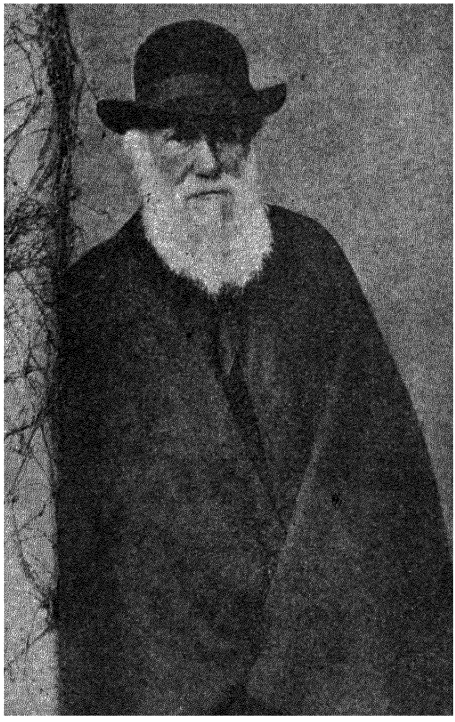


FIG. 42.—Charles Darwin.

shows that no species is increasing at any such rate, and a simple calculation shows that room on the earth would not be available if they did so increase. By far the major portion of each generation does not survive to the reproductive period. Darwin conceived the most important consequence of the potential increase in numbers to be a merciless competition among the members of the species. Any qualities possessed by an individual which gave it an advantage over others in this competition would, he concluded, insure that it would be among the survivors.

On the supposition that its peculiarity would at least often be inherited, the next generation should include a larger proportion of individuals exhibiting the advantageous character. With repetition of the selection each generation, all survivors should eventually be of the favored type; that is, the whole species would have changed in this one respect. During the progress of the change other characters might also be involved, and different niches of the environment would select differently. Consequently there would be a continuing evolution, with a division of species into several or many species.

It will be observed that this theory of natural selection is concerned only with the direction of evolution. It takes variation for granted. Darwin knew nothing of mutations as definite changes in units of the genetic mechanism, but he shared the common knowledge that individuals of a species are seldom precisely alike. He was aware that some of these peculiarities are not transmitted, but never quite grasped the fundamental distinction between a class of inherited modifications (mostly those which are now called mutations) and another group of temporary alterations which are due to environment in a broad sense.

One of the principal arguments advanced by Darwin in favor of his theory, aside from the forcible logic of it, was the remarkable history of artificial selection. Breeds of domestic animals of all kinds and a great variety of cultivated plants had responded with an extraordinary amount of change to the conditions imposed by man. While recorded history included only a small part of this change, domestic animals were so different from any wild species that none of them could be supposed to be a mere unaltered importation from nature. The method of the breeder had been that of selection, and the changes had been in the direction of the selection. Surely heredity could be relied upon as fully in the wild as in breeding pens, so that if something natural could be found to supplant the breeder as a selective agent, the general consequences of animal and plant breeding should be duplicated under natural conditions. That selective agent Darwin believed to be the usefulness or harmfulness of the qualities of the animals themselves.

This very brief outline of the Darwinian theory will suffice for an examination of its validity, to which we may proceed.

Is the Struggle for Existence Real?—One of the first inquiries concerns the actuality of the struggle for existence. No exception can be taken to the arithmetical calculation which shows that, but for enormous losses, any species would quickly overrun the earth. It is not at once clear, however, in what manner the destruction is brought about. If the struggle for existence be thought of as a competition among individuals of the same species, it is probably less important than Darwin supposed it to be. Probably no species has ever reached the point at which its members suffer lack of room. Even the hordes of grasshoppers that were the plagues of biblical Egypt as well as of modern agriculture have not wanted space to settle or even to fly about freely. Occasionally the members of a species become so numerous, at least over part of its range, that they practically exhaust their usual foods. These epidemics are not common, however. It would not be safe for a species to indulge frequently in such exuberance, except in small areas. But the danger inherent in frequent overproduction is not what prevents it; it is merely an indication that such excesses must be infrequent inasmuch as they are not fatal. Presumably some competition of the sort Darwin postulated arises in times of epidemics of overproduction; but is it likely that selection occurring infrequently would weigh heavily as compared with other factors working all the time? The major reason for reduction of numbers must presumably be found in something else.

If the struggle for existence be regarded merely as the skirmish of the organism with its environment, the element of competition is not involved. In the combat with external conditions, large numbers may be destroyed about as easily as small ones. If a machine gun be swept over an enemy position in which only one man is exposed, the loss of life will be slight; but if a whole regiment is in the open the carnage may be terrific. The environmental agent is the same in both instances. If a spring torrent rages through a gorge in which only a dozen insect larvae of a certain species exist, not many can be lost; but if millions are present, millions may be destroyed. When a temporary pond dries completely the amount of destruction depends on how densely it was peopled. Toxic substances discharged into a stream or lake kill many or few, depending on what numbers are exposed to them. In other words, destruction

by environmental conditions is largely in proportion to numbers of individuals in existence. There are many sources of danger to organisms. In the aggregate they constitute an effective curb on numbers of living things. There are enough of them that species seldom reach the competition stage. This does not mean that there is no natural selection. It merely means that the struggle for existence in the usual sense of competition among individuals of the same species for space and the requirements of life is not so rigorous as has sometimes been thought. We shall even do ourselves a service in clearing the way for other concepts of selection if we discard competition altogether. We can the better then look for a substitute.

Life and Death Not Sole Alternatives.—A further gain in acquiring a correct notion of selection will be made if we can dispel the notion that a species may be barred from evolving in a certain direction only by destroying the individuals that mutate in that direction. For decades after the enunciation of the natural selection theory the prevalent view was that favorable qualities enabled an individual to survive, unfavorable ones or even the lack of favorable variations caused it to perish. Critics of the theory, or of some of the applications of it, pointed out that the characters which were held to have developed in response to natural selection were often too insignificant to have had survival value. That is, they conferred too small an advantage to save the life of an individual which but for it would have died. It appeared to be taken for granted that the only discrimination which could be made between two possible lines of evolution would be the destruction of individuals leaning in the one direction. Even as late as the early years of the present century, a work canvassing the status of Darwinism at that time referred to natural selection, on page after page, as involving life-and-death distinctions. Conn, some years earlier, had pointed out the needlessness of this assumption, and occasionally others shared his view. But for a long time the prevailing assumption was that a character must save a life that would otherwise be destroyed, or destroy an individual which without that character could survive, if natural selection were to work.

What should supplant this view? To answer this question it need only be recalled that success or failure depends on numbers. Apart from the consequences of their own qualities,

individuals tend to maintain themselves in the same proportion from generation to generation. So far as the mere machinery of propagation is concerned, a type constituting a given percentage of the population in one generation may be expected to constitute the same proportion in the next generation. This statement is a little better made of the genes, as in the preceding chapter, but in the long run is true of the characters they represent. Should a certain character, by any means whatever, increase its quota in one generation, it starts on a new basis from that point. There is no *expectation*, from the operations of chance or of the modes of reproduction, that it will revert to its former less numerous representation, though it may do so. Any gain tends to be held, however it is caused. Likewise any loss tends to be perpetuated so long as nothing extraneous to the mere scheme of continuity enters to change the situation. Any increase of individuals possessing a given quality strengthens the presumption that that quality will persist. Numbers, in whatever manner attained, constitute the best assurance of permanence. Numbers are to a biological type what financial reserves are to an industrial corporation. They are what enable the type to survive occasional losses. In short, nothing succeeds so well as success.

Any quality which kills an individual or saves it from destruction must influence the relative numbers of different kinds of individuals. But any other way of influencing numbers may be very effective. Anything which increases fertility should favor the fertile type, and that may happen in many ways. It may increase the number of eggs produced, either by lengthening the reproductive period, or by speeding up the growth of the eggs. It may shorten the interval between generations and, without any increase in the number of eggs per female, enlarge the representation of that type in the course of several generations. If there is any disease which, though not fatal, hinders the reproductive processes resistance to it has a favorable numerical consequence. In mammals certain hormones control the discharge of the eggs from the ovaries and the implantation of the early embryo in the uterine wall; any difference among individuals with respect to these hormones, even though it had no influence on the life or death of the individual, would affect the numbers of the different kinds of individuals in later genera-

tions. One of the vitamins has an important influence upon reproduction in mammals, and there may well be differences in the dependence of individuals upon it, differences which entail neither life nor death.

Any advantage in numbers gained in one generation tends, if the reason for it persists as it would if due to some favorable inherited quality, to be accentuated in each succeeding generation. In each generation the death losses due to what may be called accident should strike all types of individuals in equal percentages, hence the favored types should retain their numerical advantage after such accidental elimination quite as much as before it. The advantage is thus cumulative. Even a very slight percentage increase, not necessarily occurring every generation but perhaps only occasionally, should suffice eventually to enable the favored type to supplant those less favored.

It is clear, therefore, that natural selection need not render life-and-death decisions in order to work. Mere differential numbers suffice. Recognition of this fact alters somewhat the criticisms that may be leveled against it, and conclusions regarding what it can accomplish.

The Criterion of Usefulness.—In view of the conclusion that death need not be the fate of unfavored individuals, in order to make selection operative, what sort of character may be fixed in a species by this method? "Useful characters," selectionists have said in answer. From the beginning of speculation regarding the Darwinian theory that was the answer. Conjectures regarding the origin of qualities through natural selection regularly clustered around their supposed advantages. If a use was obvious, or could be invented, the rest of the story was easy; success of the useful quality was supposed to follow as a matter of course. It will later be useful to point out specifically some of the things held useful, but for the present it may suffice to say that the pro-Darwinian literature for several decades following the publication of "The Origin of Species" was full of guesses regarding the value of characters whose use was not obvious.

While usefulness is necessary in a trait that is to be favored by natural selection, it should be clear that it must be an advantage of a particular sort. It must increase numbers of descendants. That type of individual will most influence evolution which

leaves the most descendants. A quality may be of very great service to an individual, as an individual, and have no evolutionary value whatever. It is even conceivable that a character might be harmful to an individual in one or more respects, and still be useful in an evolutionary sense to the type to which the individual belongs by increasing fertility. In our complex human society large families may not be exactly useful to a mother as an individual, but they render it more likely that she will have descendants a few generations later, and more likely that any uncommon genes which she may possess will exist in the population at that time. Among animals in general long life is by common standards an advantage; but if life is merely prolonged after the end of the reproductive period it does not increase descendants, and hence is not of evolutionary value. Rapid growth may indicate general vigor, which for the individual is a good thing; but if this vigor is not expressed in more offspring, it has no selective advantage. Any quality which enables one animal to secure its food more easily leads to a greater degree of comfort; but it is by no means certain that this is regularly translated into an increased progeny. Everywhere and always the selective value of a character is measured by its influence on the number of descendants its possessors will have.

The Characters Regarded as Useful.—In the literature of Darwinism the characters supposed to have originated through natural selection have, until lately, fallen largely into four groups. One of the most common is the category of traits which enable the individual to capture its food most readily. In one evolution treatise written in the present century the leaves open at the example of the long neck of the giraffe, supposed to be an advantage in reaching for higher leaves in times of scarcity. Hundreds of other examples of food-getting capacities have been cited as results of natural selection, revealing a belief that food is not only one of the most important requirements of animals, but one of those most frequently missing or inadequate. The latter feature of this belief may be seriously questioned. Starvation is probably not one of the very common causes of death among animals in general. Trees are occasionally denuded of their leaves by caterpillars, and there is doubtless some starvation among those individuals not yet far enough

advanced to pupate. What effect has this had on the species? Has it developed in the caterpillars an ability to live on the bark instead of the leaves, or on the leaves of some other plant? There seems to be no good evidence that this is true. If the advantage possessed by some individuals was merely that of being able to seize the last remaining bits of green leaf ahead of some of their fellows, success must often have involved scurrying from point to point over the tree, at random since the caterpillars probably do not see far. But granting that there are deaths from starvation, and that some of these are selective, it still is almost certain that food getting as a selective process has been greatly overburdened.

Ability to escape from enemies is another of the common qualities which have been attributed to natural selection. It is supposed to have originated in many ways. In some escape is held to be due to agility—fleetness on land, swift flight in the air, speedy swimming in water. In others it is resemblance to surrounding objects, causing them to be overlooked by predatory animals. The dull colors of some birds, the mottling of frogs, the green or brown colors of insects seen against leaves or bark, are examples. In still others it is held to be the habits, such as death-feigning, which save individuals. While escape from enemies is assuredly conducive to more descendants, it is at least permissible to doubt some of the supposed means of escape. It is by no means clear that objects concealed from human eyes by resemblance to their surroundings are equally concealed from the eyes of predatory animals. And in any case, one may suspect that a census of the causes of death in animals would show the number killed by predators lagging far behind other deaths partly due to the animals' qualities, some of which are suggested below.

Resistance to environmental conditions, largely climatic, was a third favorable trait commonly supposed to have arisen through natural selection. It took many forms. Individuals unusually able to withstand desiccation were thought to have enabled aquatic animals first to conquer the land, and then at a later stage to invade the deserts. Ability of a few individuals to endure low temperatures accounted for the establishment of new species in the near-polar regions. The opposite variation of some individuals led to the peopling of hot springs with minute

organisms. Variation in the reaction of aquatic animals to the salt content of the water led to migration, on the one hand into fresh-water bodies and on the other to exceptionally saline waters like those of Great Salt Lake which is five or six times as salty as the ocean. While the examples so far cited are mostly such as would enable animals to spread into new regions, perhaps evolving new species as they did so, the same abilities were looked to to save the race in times of unusual hardship. Extraordinarily cold weather might destroy all of a species but a few variant individuals; and subsequent generations were assumed to be of the same resistant kind. Stronger flight in a few members might save an insect species from destruction in high wind, or a better method of clinging to fixed objects might save them from wind or strong water currents. But examples need not be multiplied.

The other principal type of advantage which is referred to in the literature of selection was appeal to the opposite sex. This particular form of survival of the fittest is more appropriately described in the next chapter along with several other supposed special forms of selection. But it may be said here that many supposed examples of it were discovered in the same way as most other results of selection have been found—by speculation—soon after the idea was first propounded. If occasional inherited characters of one sex which are attractive to the opposite sex operate to insure more offspring from the attractive individuals it goes without saying that the species should trend in the direction of those qualities. And naturalists of the early Darwinian period rivaled modern advertisers and scenario writers in the conviction that sex appeal is one of the most important qualities of living things.

Important Characters Not First Emphasized.—So abundant in early Darwinian writings are examples of the four kinds named in the preceding section that one has usually to read far to find those which in the light of modern biology seem more important. While resistance to disease was occasionally mentioned it was apparently not regarded as of high consequence. Today it would probably be rated as one of the cardinal properties of a successful animal. There is no satisfactory way of deciding the relative values of the different qualities. Only a census of the causes of death or of curtailed activities would make such a

comparison possible. But knowledge of the pathogenic organisms which attack animals of many kinds, and of the deep inroads which such organisms make on the species that harbor them leads to the belief that immunity or even moderate resistance to them would be of almost incalculable value. The virus wilts of certain caterpillars, nematodes parasitic on grasshoppers and some other insects, and protozoan blood parasites of various vertebrate animals will serve to illustrate this menace. The disease organisms need not kill their hosts in order to reduce numbers. They need only affect the vigor of metabolism in such a way as to curtail reproduction. There is every reason to suppose that throughout the animal kingdom different strains within any species subject to such attacks differ in their susceptibility to the infecting organism. The differences are not easy to discover, which may account for the neglect of this factor in the early speculations on natural selection—aided by the fact that the minute organisms were at that time not recognized as the source of disease.

Fertility has already been mentioned as the necessary aggregate result of all the qualities of a successful animal. No tribe can hope to triumph in the race for dominance in a species if it continuously produces fewer offspring than do other strains. This quality is mentioned again here because it is sometimes, perhaps often, a property by itself, entirely apart from any other manifestation. In a number of animals (Drosophila, for example) and likewise in plants genes have been discovered which affect fertility and are not known to have any other effect. No valuable quality could more directly enhance the prospects of permanence or universality of a certain type than the possession of such a fertility gene.

Individual plasticity is another extremely valuable property. By this is meant the ability of an organism to adjust itself to a wide range of some element of the environment, or to a great variety of factors of different kinds. A species whose members lack this quality would be obliged to present to the environment a large amount of genetic variation in every generation—or at least in every generation in which considerable fluctuation of the environment occurs. Of this genetic variability those parts which happened to fit the current external conditions would succeed, the rest would perish or at least be reduced in numbers.

It is difficult to see how, with all this elimination of the unsuitable genetic compositions, the variation could be maintained generation after generation. Contrast with this genetic variance the situation of a species with plastic individuals. Without any marked variability in the collections of genes in individuals it is still prepared to meet any likely environmental conditions. There is no problem of the loss of capacities owing to elimination of inappropriate gene combinations, for there is in general only one set of pertinent genes, and it is always ready to fit any situation. Species occupying large and diverse ranges, without any marked differentiation into varieties, must ordinarily be of the plastic type.

Accidental Destruction Urged against Natural Selection.—Despite the rather general and rapid acceptance of the evolution doctrine among intelligent people following the publication of "The Origin of Species," the indorsement of the theory of natural selection as the guiding factor was never unanimous. There have always been naturalists who regarded the theory as incomplete and of limited application. Some of their objections may now be plausibly met, others are still difficult to answer.

One of these objections related to the plainly unselective nature of accidental deaths. These accidents have been discussed in an earlier section as largely removing the competition among individuals of the same species inherent in the idea of struggle for existence. If deaths are due to accident, it was asked, how can the individuals possessing favorable qualities gain any advantage? The answer is that natural selection is not balked by accidental elimination; it still operates among the survivors. If among the individuals that escape the random destruction there are some which, because of their properties, are able to leave a larger number of descendants, the qualities which they transmit will be present in an increasing number of individuals in successive generations. The percentage advantage from this greater fertility is precisely what it would be without the preceding random elimination. Accidental destruction reduces the field in which qualities favorable to an increase in number of descendants may work, but does not prevent their working. Were there a competitive struggle for existence, natural selection might take on a very different form, and acci-

dental deaths prevent it from assuming that form; but its operation through differential fertility remains unaltered.

Uselessness Not Accounted For by Natural Selection.—The triviality of many characters of organisms was also often cited as contradicting the selection theory. Every species possesses features which nothing but imagination could endow with any use. The number of spines on a fly, the arrangement of spots on a beetle, the number of fin rays in fishes, the branching of the veins of an insect's wings will serve as examples. The differences between the species of the same genus—the so-called "specific characters"—are mostly if not wholly among the apparently useless qualities, as was pointed out in the first chapter. The early way of disposing of this objection was to plead man's ignorance, and to suggest humbly that if we knew all we should know we could see the uses to which these trivial things are put. A more refined way was adopted later when it was supposed that neutral or even harmful qualities might be in some manner correlated with useful ones, so that when the latter characters were brought to prominence by natural selection their useless correlatives were dragged to the same eminence.

When linkage of genetic characters due to the inclusion of the genes for them in the same chromosome became known, it was several times suggested that here might be the mechanism of correlation. That assumption is based, however, on a misapprehension regarding the consequences of linkage. For, after such linkage is once broken, the associated genes are kept apart as stubbornly as they were formerly held together. In the long run, as pointed out in an earlier chapter, linkage has no influence on the recombination of characters, and this source of correlation in evolution must be abandoned. Any other source must presumably be physiological. If any two characters have anything in common in their physiological basis they should be correlated. The more extensive the common element, the closer should be their correlation. Absolute correlation could be attained only if the two characters were two different manifestations of the same set of genes. No actual case of such correlation between a useful and a useless character seems to be known. Different manifestations of the same pair of genes are very common, it is true. Indeed, probably every gene has more than one effect, so that perhaps some day a real basis for

the postulated connection between a neutral or harmful quality and a beneficial one may be discovered. In the meantime, however, it seems better to admit the insignificance of many characters and seek another explanation for them.

This brief statement must suffice here, but is not an adequate discussion of the whole subject. So important for evolution theory are the useless characters that it seems necessary to devote a separate chapter to them later.

Early Stages of Complex Organs.—A further difficulty for natural selection was found in the early evolutionary stages of complex organs. No such organ as the brain or the eye or the wing of a bird could be regarded as having arisen by a single mutation in a species lacking it. The structure must have arisen gradually. Were natural selection solely responsible for its development, the steps would have to be everywhere useful. In some of these complex organs it is not difficult to imagine a use for even the slightest beginnings. That is probably true of the eye and of the brain. It is not so obviously true of the bird's wing. Indeed, it is difficult to imagine any modification of a fore leg to be useful for anything even remotely resembling flight unless it had already proceeded far toward a wing—too far to be the result of one mutation. To explain such difficulties it has often been suggested that structures changed their functions during the course of evolution, and that the early stages of complex structures were used for something totally different from their present service. Without much question such changes of function have frequently occurred; but just what the early function of an evolving wing might have been is not easy to imagine, and no plausible suggestion has ever been made. Again it must be urged that no unreasonable explanation is to be adopted merely to save a theory; the principle of change of function should not be invoked unless, in the specific instance under discussion, plausible functions can be assigned. But modern biology is not in a position to offer any completely satisfactory explanation of the beginnings of complex characters. Random shifting of gene ratios could account for some part of them but appears inadequate for the whole task. Here is one of the puzzles of evolution which appears to be still far from solution.

Coincidence of Many Harmonious Mutations Considered Necessary.—Another obstacle often said to bar acceptance of the

natural selection theory was the necessity of having a large number of harmonious mutations occur simultaneously or in quick succession. What advantage, it was asked, was increased length of leg unless added musculature was furnished? How could a beast use heavier antlers if it did not have stronger neck muscles? Of what use would the cornea of the eye be unless there were also a lens and a retina? Complex structures were analyzed into their parts, and each one supposed to be the result of an independent change of the sort now recognized as a mutation. That these mutations should all be of a kind that could work together and evolve a new type of complex structure strained the imagination even of the selectionists and caused grave misgivings as to the universal validity of the theory.

The difficulties were probably exaggerated, in that the examples cited were not always instances of independent but harmoniously interlocking changes. In all probability the one about the long leg-bones being useless without bigger muscles is magnified beyond its deserts. It is not likely that the sizes of these two structures are independently determined. If they had arisen by different independent mutations it would mean that they are now independently controlled by entirely different genes. Were that true, animals should be experiencing difficulties traceable to the same source even at the present time. In the human race, which is tremendously heterozygous, children should sometimes inherit long legs from one parent and short muscles from the other, if there is no developmental relation between the two. It is rather curious that this particular instance of bone and muscle growth could have been advanced against natural selection after the independent assortment of genes in Mendelian heredity was discovered, for it was just as serious an obstacle to the latter as to the former. What presumably happens is that developing muscle and bone keep pace in their growth. Should a mutation affect the growth of the bone directly, it is almost certain that the muscle growth would be altered to suit. There must be much more of such developmental interdependence. It is likely that branches of the sciatic nerve will always connect the spinal cord and the foot, no matter how long the legs are, and that they will not be thrown into spirals or wrinkles if the legs should turn out to be short. Much has been made, on occasion, of the internal structure of the ends

of the long bones, because the trabeculae there are set in the correct positions to meet the strain to which the bone is subject. If they owed their position to independent mutations, their arrangement would be wonderful indeed; but the fact is that their development is in response to the strains, and would be different if the stresses were different. This in itself is a marvelous arrangement, but it is a marvel of development, not of evolution—at least not in the sense described above.

The height of ineptitude of this type of criticism of natural selection was reached when it was objected that the tail feathers of a peacock could not *all* have changed in precisely the same way as a result of separate accidental mutations. While the genetic composition of peacocks is not well known, it is a safe conjecture that the tail feathers did not have to mutate independently, any more than the hundreds of thousands of hairs on the back of a guinea pig had to mutate separately and independently to produce the long-haired breed. One mutation served the latter end; and while peacocks probably changed many times before they attained their present gorgeous livery, it is likely that each of the pertinent changes affected many feathers.

Known Harmonious Mutations Not Simultaneous.—Even after dismissing the examples of characters supposedly dependent on numerous accidentally harmonious mutations which are really due to chains or groups of events related to one another and started by one or a few mutations, there are still left complex characters that are difficult to explain through natural selection. The problems of evolution have not all been solved, and these characters are among the outstanding puzzles. It may be useful, however, to reflect that the harmonious mutations need not have been simultaneous. We have seen how even harmful mutations may be carried along in a population by reason of being recessive. Now, it is known that the effect of a gene is often dependent on what other genes are present in the same individual. Indeed, it is quite probable that no gene is free from such outside interference—or aid. Under these circumstances it is conceivable that a gene which is neutral or even harmful in company with the genes which were at hand when it first arose by mutation will, in conjunction with another set of genes, prove to be useful. Gonzalez has already shown that in Drosophila the gene for arc wing increases the length of life of the individual when it is added

to a combination including the genes for purple eye and speck (spot in axil of wing). The mean duration of life of the purple speck flies was found to be 23 days; that of the purple arc speck flies was 39 days. In like manner speck increased the length of life of the arc flies; arc alone lived 26 days, arc speck 36 days. Numerous other smaller differences were obtained. The important feature of such comparisons is not length of life, however, but fertility. In this respect purple eye was the most generally advantageous mutant gene. Arc flies produced 127 offspring per pair, while purple arc produced 230. Speck flies produced 103 offspring per pair, purple speck 247 offspring. Purple is perhaps not the best example for this purpose, since the fertility of purple flies was greater than that of the wild type. Two other genes showed, however, a pertinent contrast, namely, black body and arc wing. The fertility of both these stocks was far below that of wild-type flies. Black flies produced 138 offspring per pair, arc flies 127; but black and arc together produced 149. Unfortunately these mean fertilities are based on the number of fertile pairs in each case, and the number of infertile pairs is not stated. In actual competition, therefore, it cannot be stated that the more fertile combinations just named would win. Furthermore, there is no assurance that these would be the relative fertilities under natural conditions. The latter observation is, however, beside the point, for natural conditions change and are different in different places, so that a group of characters relatively unfavorable at one time and place could be relatively more advantageous at a later time and in a different place. The important facts shown by the work of Gonzalez are that two genes in combination were more favorable than either one alone, that three genes could be more advantageous than two of them, and that no two of the genes arose by mutation at the same time. A mutant gene which accidentally became sufficiently established to exist in numbers of individuals, mostly without coming to expression if recessive, could be carried along an indefinite length of time waiting, so to speak, for the advent of another gene or other genes with whose coöperation it could become useful. The possibilities opened up by this adaptive relation of the genes to one another are endless. Until they are explored it is too early to say that any complex character is an insuperable obstacle to the natural selection theory. Like-

wise it is too early to claim that this *is* the mode of origin of such characters.

Success of Mutations in Nature.—It would be a mistake, however, to assume that mutant genes can succeed in nature only in fortunate combination with other mutant genes. It should not be taken for granted that mutations are always harmful, though most of them do appear to carry a burden of disadvantage. Not always does a mutation have to await the further mutation that will help put it on its feet. A number of mutations in Drosophila give all the indications of being approximately a match for the wild-type in the laboratory, but none of these is so convincing as one that has had a moderate success in nature. The vermilion-eye gene of *Drosophila hydei*, as reported by Spencer, succeeded to the extent of characterizing a definite portion of the fly population in a group of stores and elsewhere in an area a mile or more across. The ancestor of this group may have escaped from a laboratory, but its success, not its origin, is the point at issue. The vermilion-eyed type had not displaced the wild type, and was probably not destined to do so. But it had become so well established as to come to expression in a small number of homozygotes, and had done so in more than one local assemblage of the flies. Such inherent capacity coupled with only a slight favor of good fortune might even bring a local race into existence.

Conclusion.—In general it can be said that while the natural selection theory has not come through its crossfire of criticism unscathed, it still is not disabled. While there are things in living nature which it does not explain, it gives every indication of validity in a considerable field of evolutionary phenomena. If too much is not expected of it, it should not prove disappointing. The newer estimates of it arising out of a consideration of the Mendelian mechanism and the laws of chance have tended to heighten the esteem in which it is held, provided it be not regarded as universal in application. These things need to be said before we pass, in the next chapter, to some of the special forms which the theory has taken.

CHAPTER XII

PROPOSED SPECIAL FORMS OF NATURAL SELECTION

> Probably there is no structure or habit for which it is impossible to devise some use, and the pursuit has doubtless provided many of its devotees with a pleasurable and often fascinating exercise of the imagination. R. C. PUNNETT, 1915.
>
> Now that attention has been directed to this evidence it is found to be quite common—a good example of the fertile but, for the uncritical, the dangerous principle that an observer only finds what he looks for. E. B. POULTON, 1931.

The description of the operations of natural selection in the preceding chapter was confined to a general outline and some of the principles involved. It has seemed desirable to separate the basic scheme as much as possible from the specific examples in order that, should any of the illustrations appear less pertinent than they were formerly supposed to be, skepticism regarding the applications of the rule might not carry with it misgivings concerning the rule itself. Bearing in mind that a principle may be valid even with nine-tenths of its supposed consequences incorrectly conceived, let us turn to some of the details of animal organization which have been imputed to natural selection.

Escape through Lack of Contrast.—One of the commonest ways in which animals have been supposed to respond to selection is by becoming more and more like the general surroundings or like some particular object in the environment. The process cannot be observed going on, but the end result has been regarded as ample evidence of its existence. Predaceous animals are supposed to pass by those individuals whose mutations lead them to be less conspicuous, or more like some uninteresting object, and to concentrate their attacks on the ones which they readily perceive. Accumulation of these concealing or deceptive mutations as rapidly as the latter occur should lead to what has been called protective resemblance. This concept thus rests heavily on escape from enemies as one of the great necessities of life.

In one form, protective resemblance is similarity to the general background. Fishes, which are mostly darker-colored above than below, are seen against deep water, which is dark, by birds in the air, but against the sky, dulled by the light-absorptive power of the supervening water, by fishes or other aquatic animals beneath. Birds that nest in the midst of brownish vegetation are sometimes mottled or streaked with brown. Bright green parrots are inconspicuous in the green forests of South America. Lizards often possess a mottled gray or tawny color much like the soil, or sand, or rock, or bark of trees, on or near which they live. The pupae of butterflies are said often to assume different colors, depending on the color of surrounding objects at the time of pupation. Within certain species of small mammals there are occasionally races differing in color which live predominantly in separate regions in which the general ground color is different. Populations which tend to be isolated on white sand dunes or in regions of black lava flow are light and dark, respectively, though with variation in each area. Areas of differently colored sand are similarly peopled by differently colored mice. Sumner, Dice, Benson and others have independently described such relations and, though in various places darker pigment goes with more humid climate, all are inclined to think such differences have no simple physiological cause, but must be a result of selection. Some animals have the power to change their color, and this may render them less conspicuous. Flatfishes, which lie on the sea floor in not very deep water, change color when transferred from light sandy to coarse gravelly bottom. The transformation is brought about partly by movement of the pigment in certain cells and partly by increase and decrease of the amount of pigment, and is thought to depend on the ratio of direct light to reflected light (Sumner).

There are other instances of resemblance to some specific object in the environment. Such resemblance is thought to be not necessarily concealing but deceptive. The animals are presumably seen but are regarded as of no interest by prospective predators. A favorite example is the grayish caterpillar of a certain moth which, when disturbed, holds itself rigidly at an angle to the twig on which it rests, thus looking like a branch of the twig. Certain spiders look much like the buds of the plants on which they rest. The wings of certain insects called mantids

are green and have a net-veined structure like leaves. The Kallima butterfly of India is a famous example; the under surfaces of its wings, which are in view when the insect is at rest with its wings held erect over its back, are colored and marked in such a way as to resemble a dead leaf. Examples could be multiplied, but are needless.

Significance of Protective Resemblance.—What judgment shall be pronounced upon the evolutionary significance of these similarities? Little is really known about them. McAtee after years of study of the stomach contents of North American birds concludes that the protection is largely a myth. He gives the number of individuals of various supposedly protected and unprotected groups which were eaten, and draws the inference that all kinds are devoured about in proportion to the available numbers. It is possible to select from McAtee's lists some families which have been called protectively colored which are represented less often than would be their share in the food of birds; but there are others also said to be protected which are taken more often than their numbers warrant. On the whole the results of stomach examinations are not impressive as evidence of such protection.

Since birds are not the only predaceous animals, and since it is impossible to obtain a reliable census of the individuals of the various edible animals with which to compare the numbers devoured, we should consider other possible features of the protection theory, including its logic. Concluding that similarities to the environment or to particular objects in it have arisen through natural selection is largely conjecture—reasonable in many instances, perhaps, unreasonable in others. One may pass by the fact that the theory ascribes high importance to escape from enemies. Even if escape should prove not to be one of the most serious problems confronting a species, it is nevertheless an advantage not to be eaten. Even if resistance to disease and differential fertility have a much larger influence on the fortunes of a species, the few types which leap these hurdles are still subject to predatory attacks. Even if chance alone is responsible for most deaths, the survivors must still run the gantlet of rapacious enemies. Even if all these possibilities be realized, the selective value of escape from predators is a certain percentage

based on a small number rather than the same percentage based on a large number.

One thing needed to judge the probable value of protective resemblance as a guide of evolution is experimental determination of certain psychological relations. One important question is, is the animal under consideration really inconspicuous to its prospective devourer? It must be remembered that the visual powers of animals differ tremendously, and what is inconspicuous to one need not be so to another. Many instances of resemblance are cited without any mention of the possible enemy which is being deceived, but some of these enemies are insects. Now, it is known that at least some insects are much more aware of ultraviolet radiation than human beings are, even more aware of ultraviolet than of certain wave lengths that are visible to us. Some old experiments of Lubbock showed this to be true of ants. These insects, when their nests are disturbed, carry their larvae and pupae into dark places. Lubbock arranged his experiment so that sunlight passing through a quartz prism fell upon the area in which a colony of ants might work with red at one end, ultraviolet at the other. To a human observer the red was visible, but the ultraviolet was dark. When, however, some larvae and pupae were scattered throughout the area the ants hurriedly carried them out of the ultraviolet into the red. Obviously the ultraviolet is visible to them while red is relative darkness. Under these circumstances ants may be expected to see objects which reflect ultraviolet radiation, and to be unable to see except perhaps as dark gray those which reflect red light. Other insects have been shown by more elaborate experiments to have somewhat the same visual capacities.

How conspicuous or inconspicuous an animal is, therefore, to an insect predator may depend chiefly on how it reflects ultraviolet. No human observer can judge this quality, but Lutz has made some photographs of insects by reflected ultraviolet rays, with remarkable results. The common white cabbage butterfly appears uniformly dark, showing that it does not reflect much ultraviolet; but the white areas of the moth called the "widow" are very light in the photographs, showing that they do reflect ultraviolet. The tiger swallowtail butterfly exists, in the female, in two races, northern and southern, which

to us appear yellow and dusky, respectively (Fig. 43). In the photographs both varieties were dark (Fig. 44), showing that neither the yellow nor the dark form reflects ultraviolet well. Other insects exhibited an ultraviolet pattern which in some

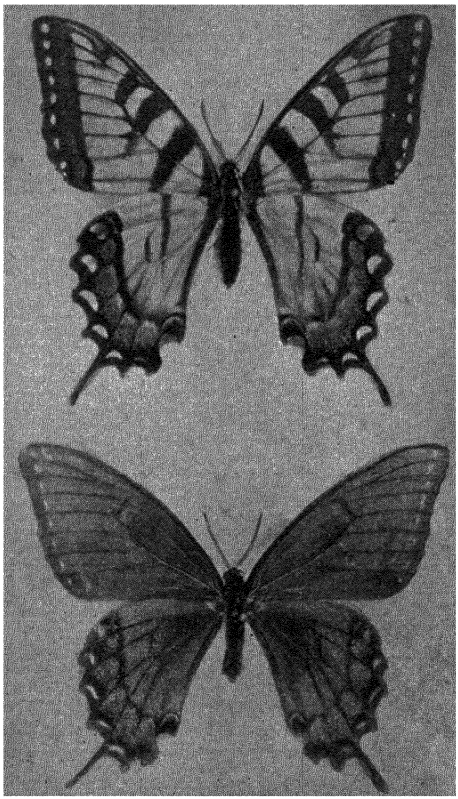


FIG. 43.—Female tiger butterflies of the yellow and dark varieties. (*Courtesy of American Museum of Natural History.*)

resembled the pattern visible to us, but in others was quite different from the pattern we see. In the Luna moth the female is as bright by ultraviolet as by "visible" light, and preserves the same pattern, while the male is dark by ultraviolet, reflecting little of the short rays except from the centers of his so-called eyespots (Fig. 45). An animal which we term inconspicuous could therefore certainly not safely be regarded as protected from attack by a predaceous insect.

Vision in vertebrate animals is probably more nearly like our own. Fortunately there is some experimental evidence that inconspicuous animals do escape their vertebrate enemies more readily than highly contrasting ones do. Sumner has rendered

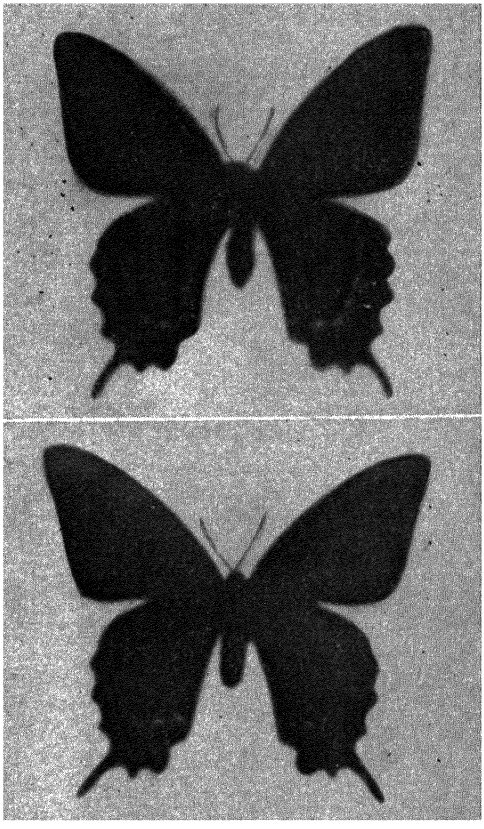


FIG. 44.—Female tiger butterflies photographed by ultraviolet: yellow variety above, dark below. (*Courtesy of American Museum of Natural History.*)

certain small fishes temporarily dark or pale by keeping them for some weeks in dark and white tanks, respectively (Fig. 46), and then feeding them to penguins and herons among predaceous birds, and to larger fishes. When the feeding was done in black-lined tanks the light fishes were taken in greater numbers, while in light gray tanks the dark fishes were most often captured. Greater agility of the light fishes might help to explain their

escape in the light tanks but would only accentuate the significance of their most frequent capture in the dark tanks; and from other evidence Sumner is convinced that differential activity has nothing to do with the unequal success of the light and dark fishes. From earlier experiments di Cesnola concluded that green or brown praying mantis was less subject to attack when

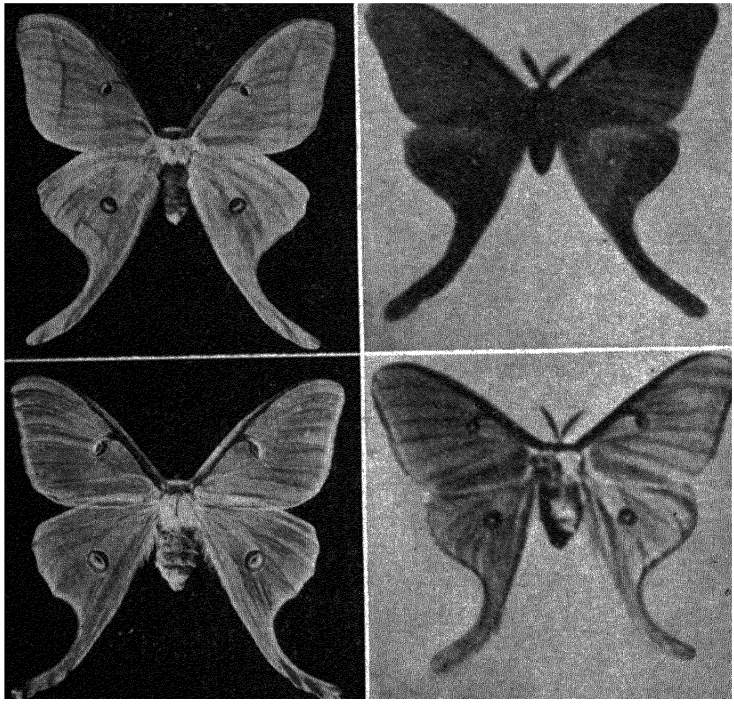


FIG. 45.—Luna moth. At left, photographed by visible light: male above, female below. At right, photographed by ultraviolet: male above, female below. (*Courtesy of American Museum of Natural History.*)

on a background of its own color, and Krausse observed each variety slightly more often on its own color; but Rabaud was unable to verify these results with the same species.

Aside from these experiments evidences of the overlooking of prey by carnivorous animals are meager. When a predator passes by possible prey it is by no means certain that the latter was overlooked, or that any item of food, however conspicuous, would have been captured at that particular moment. A census

of the individuals eaten by a given species, even if it shows that the victims are more largely of the types which look conspicuous to us, contains no real evidence that visibility was the reason for their capture. It may have been, but so also may greater palatability.

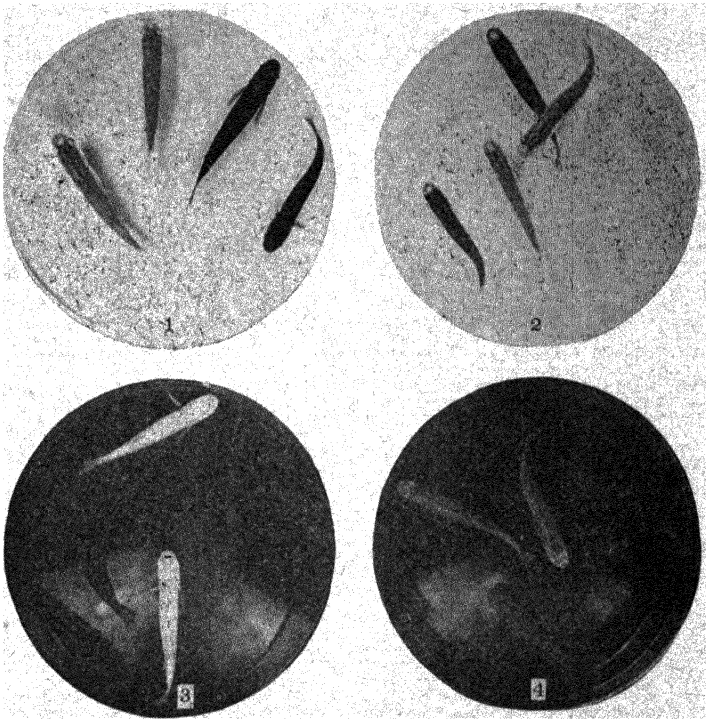


FIG. 46.—Protective coloration, experimentally demonstrated. Light and dark fishes on light and dark backgrounds were unequally subject to capture by predators. (*From Sumner in American Naturalist.*)

A factor seldom taken into account in judging of conspicuousness is the size of the object relative to that of the observer and to the latter's field of vision. A gray mottled bird perched among broken rocks is but a very small part of a very large landscape as viewed by a man, and may be difficult to see. To a weasel, which is a much more natural enemy, however, it is a relatively large object in what is probably a much smaller landscape, so that if vision is his means of recognizing prey (smell may be much more important) the so-called "protected" bird

is perhaps rather easily seen. Large objects are almost certainly much more easily seen than small ones of the same color and pattern because of the shadows inevitably thrown by them even when the coloring tends to conceal.

Citation of all these difficulties of the theory of protective resemblance is not to be interpreted to mean that color is held never to be protective, or that evolution has not been guided at all by such protection. It means simply that the notion has been overworked, that it has been applied uncritically, and that some, perhaps many, of the supposed instances of evolution guided by and leading to inconspicuousness probably are not such.

Other Proposed Guides to Resemblance.—From their historical interest mention should be made of two additional ways in which species have been supposed to be led to fade more and more into the environment. One of the alleged results has been given the name aggressive resemblance. Predatory animals were supposed to be able to creep up on their victims unobserved the more easily if they resembled the environment. Mutation after mutation, each making the similarity greater, would have to be preserved as against their alternative conspicuous characters, in order to bring about the present inconspicuousness. This claim has been made for the white coat of the polar bear; for the change of the arctic fox from white winter pelage to a brown summer coat; for the tiger whose vertical stripes are said to resemble the shadows of vegetation; and for the jaguar, a forest animal, whose splotches of color could be likened to the shadows of leaves on the objects about it.

The other similarity to be mentioned has been called alluring resemblance. Its possessor is held to be passive, not active, in its "pursuit" of prey. Instead of being able to come upon its prey unseen, it entices its prey to come to it unawares. To do this it must look, not like the general environment, but like some particular object in the environment which is attractive or of value to the prospective victim. Forbes long ago described a spider in Java which lay in wait for butterflies, which were attracted to it, he thought, because of the spider's resemblance to the excrement of birds. Red spots at the mouth of an Algerian lizard have been supposed to resemble a desert flower to such an extent that insects would approach them, only to be captured by the lizard. The theory assumes that enough advantage accrued

to the individuals which first mutated in the direction of the present resemblance to increase them in proportion to their unmutated fellows, and that these mutations were followed by others of the same sort, all proving sufficiently advantageous to be preferentially represented in later generations.

It seems unnecessary to debate at length the reality of these phenomena. All of the difficulties which stand in the way of proof of protective resemblance are obstacles to these other resemblances as results of selection, and the evidence for them is much more slender. The proposed examples of aggressive and alluring resemblance have never been put to an experimental test. Such similarities should be useful if they actually are concealing or deceptive up to the very moment of capture of the prey, but it is exceedingly doubtful whether they can be so effective. These theories must probably be set down as products of fancy belonging to uncritical times.

Warning Coloration.—The preceding sections have been devoted to striking resemblances between animals and things about them. If natural selection be supposed to be powerful enough to drive some species into such imitative appearances, what shall be said of species which are so highly colored or so flauntingly patterned as to attract positive attention? Several theories in harmony with the general principle of natural selection have been proposed and widely supported. Warning coloration is the first to be considered.

An animal which is unpalatable, dangerous or in some way protected as by spines, hairs or hardness, and is at the same time conspicuously colored, is said by proponents of the theory to be warningly colored. Professor Poulton, who is today probably the most ardent advocate of this doctrine, points out that, to the animal thus disagreeable, it pays to advertise. Quick recognition of the obnoxious species should, it is said, save its members many experimental or ignorant attacks. The ancestors of the brightly colored species of today must have been dull, and have approached the present condition step by step through the accumulation of brightening mutations, each of which must have been recognizable by predatory animals. Among the many species regarded by some naturalists as warningly colored the following may suffice as examples. Bees, wasps, yellow jackets and hornets, whose unpleasant quality is well known,

are either conspicously marked by yellow or white bands or have a brilliant metallic luster. The skunk is broadly marked with white bands. Coral-reef fishes of many species are brilliantly marked with red, yellow and blue and have been regarded as objectionable in taste. The Gila monster, the only lizard which is poisonous, has broad irregular bands and spots of black and salmon-pink. The Colorado potato beetle with its (to us) unpleasant taste and nasty reflex bleeding is conspicuously striped in colors. Poulton considers ants to be disagreeable insects and plainly recognizable as such, though conspicuous marking is not common. The lady beetles are all gaily colored, and some early experiments were regarded as proving them distasteful. The harlequin bug with an offensive odor is black with bands of red, orange or yellow. Blister beetles are the source of a drug so powerful that one grain is fatal to a human being, and some species are striped or margined with color; even the uniform black color of other species is regarded as making them conspicuous. The chinch bug so destructive to grains has what an entomologist calls a "repulsive smell and taste," and is blackish with snow-white wing covers. Also among the butterflies and moths are many described instances, but these are being reserved for the account of mimicry which involves warning coloration.

Warningly colored animals are described as going about boldly, caring not who sees them, even parading their conspicuous colors or patterns. The oftener they are seen, the less chance predaceous animals have of forgetting the association of bright colors with unpalatability. Some advocates of warning color permit one to assume that the thing remembered by predatory animals is the particular color or pattern of the obnoxious species; others, including some of the most eminent of them, would regard any bright color as a signal to predators to beware.

Weaknesses of the Warning-coloration Theory.—Certain observations are difficult to harmonize with the theory just outlined. It is possible for animals to acquire bright colors without any reasonable chance that they are warnings. Certain marine annelid worms have been included among warning species, but among the brightest of them are tube-dwellers which have no chance to display their colors. The walking-stick insects have an acrid taste, but are so dull and sticklike that they are almost

universally named among the protectively colored animals. One family of beetles (Endomychidae) is highly colored, but its members are seldom seen, since they live in fungi. This retiring habit is not what one is led to expect of the possessor of a warning pattern. Furthermore, if the first mutations which tended to make the originally dull animal conspicuous were recognizable by predaceous animals, it is difficult to see how the prey could be forced to become so much more conspicuous. If they were fully recognizable as unfit to eat at a lower stage of color evolution, they could hardly become more recognizable by becoming still brighter.

The above are merely logical difficulties. Let us see now how protective some of the conspicuous colors and other qualities are. Since more instances of supposed warning colors are found among the insects than in any other group, and since birds are some of the chief feeders upon insects, McAtee's studies of the stomach contents of birds should furnish valuable information. The chinch bug was eaten by 29 species of birds, three of which (bobwhite, meadowlark and brown thrasher) indulged in it to the extent of more than a hundred bugs at a single meal in certain individual birds. For predatory animals which are supposed to learn to avoid distasteful articles of diet, these are large numbers. Either the birds do not find the chinch bug disagreeable, or they do not learn. Epidemics of the harlequin bug are reported by a state entomologist to be held in check by English sparrows. Of the blister beetles 77 individuals were taken at one meal by a single kingbird. Lady beetles, which were once thought to have been proved distasteful, were eaten about in proportion to their numbers among insects in general. The Colorado potato beetle is not separately given in the quantitative list, but the family to which it belongs and which is as a whole regarded by warning colorists as protected, was taken somewhat more frequently than its relative abundance justified. Moreover the Colorado potato beetle is eaten by other animals than birds, many of which can see its colors and some of which should be able to learn—by poultry, skunks, snakes, frogs, toads, 10 species of predaceous bugs, 15 species of beetles, robber flies, spiders, wasps, harvestmen and mites. Something else than its protection from enemies is saving the Colorado potato beetle. Ants also are considered by Poulton and others to be in some way

recognized as distasteful and therefore avoided; but McAtee's studies show one of the most abundant families of ants to have been eaten more than three times as often as it should have been in proportion to its numbers, and the next most abundant family nearly seven times as often. The wasp family slightly exceeded its quota, and bees were taken more than half as often as their numbers would entitle them to be captured. The latter figure is almost certainly too low since, as in all these lists, there was an even larger number of insects recognized as beelike but not in a condition to be allocated to a certain family.

The theory of warning coloration was advanced at a time when little was known of the feeding habits of animals. Never since then has there been any experimental attempt to ascertain these habits on anything like the scale of McAtee's determinations of the natural food of birds. It must be said that from this source there is little evidence of the supposed protective value of conspicuous color. And only once has there been any serious attempt to study experimentally any single group of alleged warning colors from every pertinent point of view. It is worth while to examine this attempt.

Experiments of Reighard with Coral-reef Fishes.—The experiments referred to are those of Professor Reighard upon the brilliantly colored and patterned small fishes of the coral reefs off the Dry Tortugas Islands. These highly conspicuous fishes have long been cited as important examples of warning color. That they are conspicuous seems certain, for the background formed by the reefs is of subdued color broken only by shadows. That they are not aggressively or alluringly colored is assured by the fact that nearly all their food consists of sightless invertebrates which are fixed and cannot escape. Their brilliance cannot be due to sexual selection (page 194), for the sexes are equally colored. These small fishes seldom move far from the reefs and in that region are not attacked by predatory animals.

The most common predatory fish in this region is the gray snapper. Its ordinary food is a small inconspicuous fish (Atherina) which does not confine itself to the region near the reefs. It is with the capacities of the gray snapper that the experiments chiefly deal. Any predator under whose influence warning color evolves must be able to discriminate colors, and must have a memory. By tossing artificially colored atherinas (chiefly

red and blue, but also yellow, vermilion, green and purple) to the snappers it was shown that the snapper possesses both these qualities. The red fish were made disagreeable by sewing into their mouths pieces of the tentacle of a jellyfish, which is filled with stinging cells (Fig. 3, page 16). The red fish were taken promptly at first, hesitatingly later, and finally were rejected. When this association between color and stinging cells was established, the jellyfish tentacles were omitted; but the red fish were still rejected. The blue ones were being taken quickly all this time. The experiments were then discontinued for three weeks, but at the end of that time the red fishes were still rejected. It is clear from these results that the gray snapper can distinguish color and can remember. It is the sort of predatory animal which should lead to warning coloration in its prey.

Now, some of the highly colored reef fishes of several species were collected and tossed (some alive, some dead, some made unconscious and motionless by pithing) to the gray snappers near the shore, which was at a considerable distance from the reefs. They were eagerly eaten by the snappers, not just in one trial, but repeatedly. The few that escaped did so either by their agility or by reason of their being the less conspicuously colored ones, the latter fact indicating that dullness, rather than brightness, would have been useful to them. The brilliant fishes are not after all disagreeable to the gray snapper; and yet, in the vicinity of the reefs, they are not molested. The reason appears to be that the gray snapper takes its prey only with a swift rush, and in the neighborhood of a large solid object like the reefs it dare not assume the risk of injury.

Immunity Coloration Substituted for Warning Coloration.—Professor Reighard proposed in place of warning color a theory of immunity color. He assumed that, since color had developed far beyond the point at which it would be completely useful even if it were a valuable warning, it must be due to some innate tendency and not to selection at all. The possibility of an internal force of some kind which carries evolution along without reference to any usefulness of the changes is discussed in a later chapter (XV). If highly colored animals possessed such a tendency, then dullness rather than brilliance would be the thing that called for an explanation. Such animals would be

bright unless there were a reason for being inconspicuous. Assuming predatory animals to be their chief danger, and in the absence of any quality or special situation which protected them, they would have to have developed protective coloration (dullness as a rule) or have perished. Only those animals which had some other protection could afford, he thought, to develop color in accordance with their innate tendency. Coral-reef fishes, having the reefs for protection and the habit of staying near them, could do so. There was in their evolution no pressure of selection toward dullness; that is, they were immune to the agency that would lead to protective resemblance.

Reighard applied the theory of immunity coloration to other instances of supposed warning color. Where, as was so often assumed to be true of insects, a species possessed a disagreeable quality, that property would be the thing which made the animal immune to the pressure toward dullness. Any other property which would make inconspicuousness unnecessary would lead to color, provided the animals possessed an innate tendency toward color. It will be observed that this theory rests primarily on the validity of the theory of protective resemblance. If the latter theory is of only slight validity, that of immunity coloration is correspondingly weak. Reighard's theory also assumes that warningly colored animals do actually have some disagreeable property. If they do not, they must have some other protective quality which makes inconspicuousness needless, or immunity color cannot have arisen as he postulated. As will be seen in the previous sections the theory of warning color is of doubtful validity, and protective resemblance may be less important than it was once believed to be. The idea of immunity coloration is therefore on a less secure foundation than it at first seemed.

Mimicry.—Another method proposed to account for conspicuous color in animals is that of mimicry. In the original form of the theory the mimicking species is supposed to be edible, but to resemble another species which is distasteful or is otherwise protected from predaceous animals. The disagreeable species is ordinarily supposed to be conspicuous, that is, it is warningly colored; hence mimicry is conspicuousness in an edible species which imitates a warningly colored species.

The ancestors of the mimic are supposed to have been dull. How rapidly any of them came to resemble the warningly colored animal (the model) is a moot question, but the originators of the mimicry theory and its most ardent supporters today conceive the change to have been a gradual accumulation of likenesses. If this were the method, it must be supposed that one or more members of the dull edible species developed a small amount of color which resembled that of a brilliant inedible form—resembled it enough to deceive predaceous animals into thinking them not good to eat. Such individuals would have an advantage, and would transmit their color to succeeding generations. Further color mutations might arise among these colored descendants, accentuating the likeness to the warning color of the model, and these would again be selectively favored. Eventually the high degree of similarity now exhibited by the mimic would be developed, always through the action of selection.

There are many examples of similar patterns and colors which have been regarded as instances of mimicry. The bulk of them are among the butterflies and moths. In North America one of the chief examples is that of the viceroy, a large brown butterfly, which resembles the monarch, a still larger brown species belonging to another subfamily. The viceroy is held to be the mimic, the monarch the model. Most of the butterfly examples are, however, in tropical regions of South America, Africa and the Orient. Sometimes three or more species resemble one another, constituting so-called mimicry rings. Sometimes in such rings the females resemble the supposed model while the males do not. There are many grades of complexity in these rings, and many examples of some of the types. Most instances of mimicry in butterflies occur in a certain small group of subfamilies. Any one interested in the details of specific cases should consult Poulton's "Essays on Evolution," 1908, or his articles in the *Transactions of the Entomological Society of London* or Punnett's "Mimicry in Butterflies." Among the less numerous examples outside the butterflies and moths are the alleged mimicking of the lady beetles by other beetles, of a beetle by a grasshopper, of a wasp by a beetle, of the honeybee by a fly, of a wasp by a moth, of an ant by a spider, of a snake by another snake and of the friarbird by an oriole.

Two Kinds of Mimicry.—These examples of mimicry are supposed to fall into two categories. The original proposal of mimicry was made by Bates in the early eighteen-sixties, and was of the sort described in the preceding section. In it an edible species mimics an inedible one. This type of mimicry is known as Batesian mimicry. Later a difficulty arose in the discovery that different species in the same subfamily resemble one another. Now, it is held in general that all members of one subfamily are edible, or that all are inedible. The discovery of a pair of similar species in one subfamily meant, therefore, that one distasteful species was mimicking another distasteful one, or that each was mimicking the other. On the Batesian scheme it was difficult to see how that situation could arise through natural selection; for, if a species was already immune to attack by reason of its disagreeable qualities, it could not well be helped any by coming to resemble another immune species. Fritz Müller came to the rescue by suggesting that two distasteful species might economize by offering to predatory animals only one sign of distastefulness instead of two. Predators would have to learn by experience that animals having a brilliant color were not good to eat, and in learning would destroy a certain number of individuals. If this loss could be divided between two species it would be an advantage. Since birds are believed to be the chief enemies of butterflies, Punnett has called it concentrating on the education of young birds. Müller supposed this to be the way in which selection made the two species alike; and so, similarity between two inedible species has come to be called Müllerian mimicry.

Most believers in mimicry theories hold that both these types of mimicry exist, but there is a strong tendency now to adopt the Müllerian view. Many instances formerly supposed to be Batesian mimicry are now regarded as Müllerian, and the strongest advocates of the general theory consider Müllerian cases to be the more numerous. It is clear from these changes of opinion that the distastefulness of the species is not actually known, but is being inferred from other facts.

Characteristics and Rules of Mimicry.—Wallace, who was one of the early supporters of the mimicry doctrine, listed a number of characteristics which he said all instances of mimicry exhibited. These characteristics have been generally adopted as rules by

which the relations in any example of mimicry could be judged. For frequently, as just intimated, it is not known which—if either—of the similar species is distasteful, and hence which is the mimic, which the model. That is, more often than not, there has been no experimental test of the qualities of either species.

The first of Wallace's rules was that the resembling forms occupied the same area. If they did not, any unpleasant experiences of predatory animals in the area occupied by the disagreeable species could not very well redound to the advantage of the individuals in the other area. Next, there is a difference between the species in their liability to attack, one being more protected than the other by its own qualities. This rule applies primarily to Batesian mimicry and perhaps not to Müllerian mimicry at all. Further, the model is more numerous in individuals than is the mimic; it needs to be so if predaceous species are to get their prevailing impression of disagreeability from animals having the bright colors in question. Also, the mimic has a distinctly different color or pattern from its near relatives. Otherwise its color is a mere matter of heredity from the ancestral type and there is nothing remarkable to explain. Lastly, the imitation affects only the external visible characters; to arise through selection the likenesses must be such as can be seen by predaceous animals.

These necessary conditions have been made the basis of some of the criticisms leveled against mimicry. We may now turn to the various objections raised in an attempt to judge the validity of the whole scheme. The criticisms are grouped, but there is much overlapping of the classes.

Criticisms of Mimicry Relating to the Resembling Species.—One of the serious weaknesses of the theory of mimicry is that in so many of the supposed instances of it there is no real knowledge that one of the species is protected by a disagreeable or dangerous quality. Such a quality is rather obvious in bees, wasps and hornets, and in some snakes. Feeding experiments have not been numerous, and have usually involved few individuals, and little attention has been paid to the pitfalls of experimentation with animal behavior—one of the most difficult fields of biology. Plate fed a few warningly colored butterflies, mingled with many others, to a lizard, and the dull ones all succumbed before the warningly colored ones. The bright butterfly used is regarded as

the model of another species. Poulton points out that among a large number of moths eaten by bats less than one per cent were conspicuous, but neglects to state in what proportion these conspicuous ones were available to the bats. One wonders, also, just how visible the colors and patterns are to these night-flying mammals. Moreover, where ants are the supposed models it is doubtful whether that status can be maintained for them in the face of McAtee's discovery that some ants are eaten three to seven times as frequently as their numbers entitle them to be. One ant specialist voices more than a doubt by saying that whenever an insectivorous animal gets hungry, the first thing it thinks of is an ant.

In a few instances animals have been regarded as mimic and model when they belong to the same genus. The incentive in such cases is sometimes the existence of similar races in each of the species. One entomologist regards two species of the butterfly genus Heliconius as a mimicry pair (Fig. 47). In each species there are three races, and each race of one species is very much like one race of the other species. It would seem as if two species of the same genus might resemble one another simply because of their kinship. And as for the races, we are already familiar from an earlier chapter with the occurrence of corresponding mutations in different species of Drosophila and in various small mammals which are not so closely related as these butterflies. Directed mutation could easily account for the similarity of the races.

Much has been made of the fact that a single type of resemblance may be arrived at in apparently different ways. An example is the transparent wings of a number of species of butterflies. The opacity and pattern of color of the more usual butterfly wing are due to hosts of pigmented scales ordinarily laid flat. Now, in some of the clear-winged mimics the transparency is due to reduction in the size of the scales, in others to reduction in number, in others to lack of pigment in the scales, and in still others (at least so it seems in dry museum specimens) by having the scales set up on edge. It is argued that if the same functional result can be arrived at in so many structural ways there must be some deep-seated method at the basis of them, and that method must be selection of modifications advantageous from a purely visual standpoint. It is not so certain, however,

that the clear wings are as different fundamentally as the comparison indicates. Reduction in size and number of scales, and even their vertical placement, could all be due to the same growth mutation, acting differently in different species because of the different other genes present. Genes are well known to have different effects depending on the other genes occurring with them, and corresponding mutations occurring in even

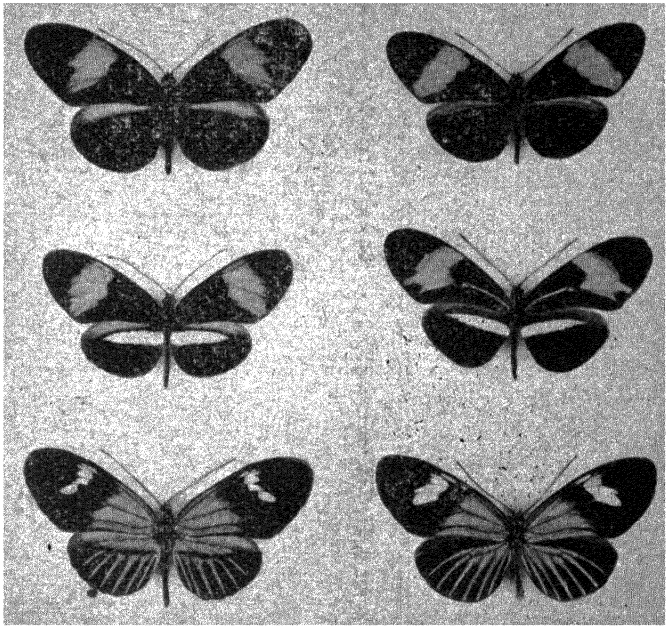


FIG. 47.—Two species held by some to be a mimicry pair notwithstanding that they belong to the same genus. Left, *Heliconius melpomene;* right, *Heliconius erato.* In each species there are three varieties, similar to those of the other species. (*Courtesy of Ward's Natural Science Establishment.*)

rather distantly related animals are also well known. Even reduced pigmentation might depend on the same mutation as reduced growth. Growth is known to modify other characters which are not merely differences in size, as is pointed out in Chap. XV, and could easily have such an influence on butterfly scales.

Criticisms of Mimicry Relating to the Predaceous Animals.—Another group of objections urged against mimicry has to do with the enemies from which the mimics are supposed to be protected. Owing largely to the aerial habits of butterflies, the

birds have been almost universally pointed to as the chief predators of that group of insects. Are the birds important enemies of the butterflies? The paucity of feeding experiments has already been mentioned. Possibly also it may be said that such experiments have seldom included the safeguards that psychologists insist on erecting around tests of other features of animal behavior—one of them the safeguard against subjective error. All of them combined can hardly have the weight that McAtee's stomach content examinations have, for stomach contents are acquired under natural conditions, and it is under natural conditions—if any—that birds influence mimicry. McAtee examined the stomachs of 80,000 birds. In them he found 87 adult butterflies, 69 of them in one species of bird, the pigeon hawk. There were many more larvae than adults, and many more moths than butterflies. Since the theory of mimicry has dealt much more with adults than with immature stages and much more with butterflies than with moths, it seems necessary to confine consideration to the 87 specimens. Had it not been for the pigeon hawk the number taken would be insignificant. McAtee concludes as a general proposition that animals are eaten about in proportion to their numbers; but in this instance he must be thinking of all Lepidoptera, not just butterflies, and of immature stages, not just adults. The adult butterflies can hardly be as small a proportion of our insect fauna as they are of the stomach contents of most birds. The only other inference that seems possible is that the butterflies are spared. It is unfortunate that the stomach contents do not reveal whether the monarch and viceroy were represented, but a proportion based on so small a number would have little value. It is likewise unfortunate that a study of bird stomachs can not be made in the tropics.

When the natural enemies of mimics have been correctly ascertained, it is in order to inquire whether their activities are those which would develop mimicry. Even if birds be potent enemies of the butterflies, it is not certain that they see colors and hence patterns as we see them. Some experiments by Hess on domestic fowls indicate that the middle-to-red portions of the spectrum are more easily seen than are the blue and extreme red. Until more is known of bird vision it is not precisely safe to say that mimicry devised to fit human capacities will work when natural enemies of the mimics are substituted for man.

Another doubt expressed regarding mimicry is whether the similarities are sufficient to deceive. Punnett observes that museum specimens are sometimes more alike than living ones. Bodies which may be brightly colored are distended in the living butterflies but shriveled in dried ones. In one particular case of mimicry in which the model has a scarlet body, but the mimic no red of any shade on the body, he admits that he might be fooled in the museum, but not in the jungle. Poulton describes the capture of a clearwing moth (supposed mimic of a hornet) by a lizard which, at the first trial, carefully kept away from the "stinging" end; but discovering the moth to be harmless after all, the very next time a clearwing was offered the lizard recognized its true nature and ate it without caution. If a single experience is all that is necessary to see through the deception, the mimicry can not be very valuable.

Aside from birds, the chief other enemies in relation to whose attacks mimicry might arise in butterflies are, according to suggestions offered, predaceous insects, the lizards and perhaps the monkeys. The predaceous insects referred to are the mantids, dragonflies, dance flies and robber flies. There is nothing in the behavior of any of these to suggest that they avoid bright colors. Lizards are known to be largely insectivorous, though little is known as to the share which butterflies have in their diet. Some experiments by Manders indicate that they eat the supposedly evil-tasting butterflies as readily as the palatable ones; and the observation of Poulton described above makes it probable that the ordinary deceptions of mimicry are in any case no match for their powers of perception. Monkeys were suggested presumably because they are numerous in regions where supposed mimicry abounds, and there is some testimony that they do actually eat butterflies. How important they may be as guides to mimicry is uncertain. Punnett discusses this subject in his "Mimicry in Butterflies."

Whatever be the enemies of butterflies or of any other supposed mimics, some naturalists have pointed out that they are called upon to have very contradictory qualities. If most advocates of mimicry are right, the resemblance has arisen by many small successive steps under selection. Under these circumstances, when the then dull ancestors of the mimic-to-be first mutated in some slight degree toward the color of a distasteful

species, predaceous animals are supposed to have been deceived, though the difference between the mimic and model must then have been much greater than that between the incipient mimics and their unmutated fellows. Later when the whole mimicking species has approached much nearer to the model, predatory animals are supposed to be deceived only by those individuals *most* like the model and to devour all those less similar to it. In other words, the predator's powers of discrimination must be supposed to have improved enormously, and to have been very unequal originally when the mutant individuals were compared with their kin and with the model. It would be one of the marvels of evolution if the improvement in discrimination required should have been timed to coincide so completely with the development of some mimic. This difficulty was seen by some advocates of mimicry, and it was suggested that perhaps, when this approach of one species toward the other began, they were not so very different. The ancestors of the model itself were held to be less brilliant at that time, and as they developed their warning color the mimic developed its deception. This view seems not, however, to have been generally adopted.

Logical Objections to Mimicry.—There remain a few criticisms of mimicry which rest rather on logic than upon any body of facts. First of these is that mimicry involves warning coloration. The evidence of that phenomenon was found to be insufficient to lead to conviction. If to warning coloration there be added the possible mimicking by other species, which we have just seen is very doubtful, we have a chain which, paradoxically enough, may prove to be weaker than its weakest link.

Occasionally a mimic is more abundant than its model, contrary to one of Wallace's rules. This is not a fatal objection, for it could be urged that one unpleasant experience in three or four trials would be enough to prevent attacks by a cautious predator, or it might be assumed that after the imitation was developed the model species became reduced for other reasons than predatory animals.

A greater difficulty is found in those few instances in which mimic and model do not occupy the same area. In South Africa is a supposed mimicry pair, the two species of which come together only in one small region in Angola. In Ceylon is a pair which occupy the same region as it would appear on a small-

scale map, but the model is a lowland species while the mimic is found at elevations of several thousand feet. Here migrating birds may be (and have been) appealed to to get their experience in one region and apply it in another. It is not easy, however, to explain two other pairs of species which would surely both be regarded as instances of mimicry if the species lived together, but in each of which one species is in South America, the other in Africa. There are not many instances in which the resembling species are in different areas, but they create a difficulty not yet solved in terms of mimicry.

Again, there is in South America an extensive mimicry ring supposedly of the Müllerian sort, since the resembling species are all members of subfamilies which are regularly conspicuous and supposedly distasteful. While certain of the species appear to have changed their colors, they have, according to the theory, merely changed from one warning color to another. It is not easy to imagine any considerable advantage deriving from such a transformation.

Lastly, there is some indication that mimicry may develop in part without relation to the powers of vision of the predatory animals, in contravention of another of Wallace's rules. It is well known (pages 169*ff.*) that the pattern of insects as seen by ultraviolet radiation is not necessarily related to the pattern which we see by the somewhat longer waves. Were there any doubt about this principle, its correctness would be attested by the example about to be described (Lutz, 1933). The butterfly *Planema aganice* (Fig. 48, top) is held to be the model which two other species, *Pseudoacrea tarquinia* and *P. imitator*, have copied. This is the way they appear to man, and since birds seem to have no more capacity for seeing ultraviolet and infrared than we have, the illustrations no doubt represent approximately what birds see. When these butterflies are photographed in ultraviolet, however, they appear as in Fig. 49. The males are dark and practically without pattern in all three species, while the females appear much as in visible radiation. Here are two mimics imitating (in the male) a characteristic of their model which their bird enemies cannot have detected. Since ultraviolet patterns sometimes do and sometimes do not correspond to "visible" patterns, it would be possible for the males of the three species to be unlike in ultraviolet, but similar in the

"visible," and still constitute a good case of mimicry. Apparently the similarity of the three species in ultraviolet must be explained by something else than the visual powers of their enemies; but if such an explanation is to be sought for the ultraviolet pattern, we should be quite willing at least to look for another explanation of the pattern visible to birds and man.

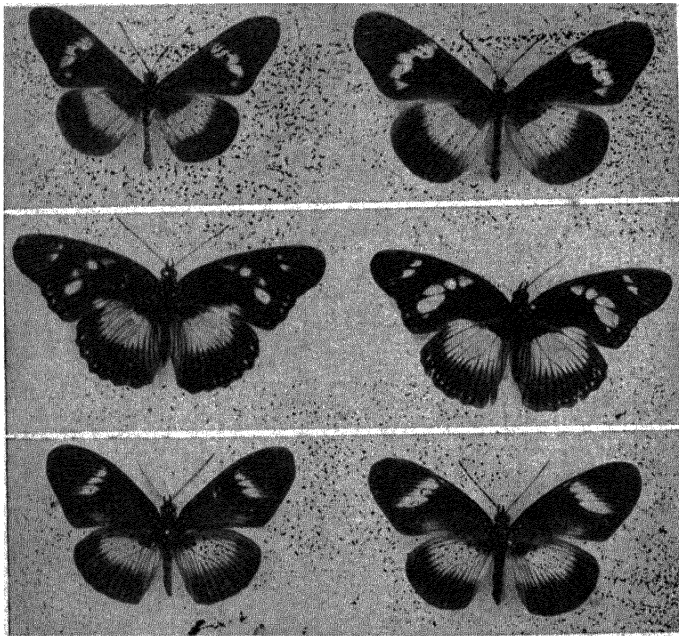


FIG. 48.—Supposed mimicry. Top, *Planema aganice*, the presumptive model; second, *Pseudoacrea tarquinia;* bottom, *Pseudoacrea imitator.* (*Courtesy of American Museum of Natural History.*)

Known Genetic Facts of Mimicry.—Many of the questionable interpretations of mimicry discussed in the last few pages would be less obscure if the genetic relations of a number of mimicry pairs and rings were thoroughly understood. It needs to be known how different from their dull relatives and from their brilliant models the mimics really are in terms of genes. The former of these relations is the more important, and should be the more easily ascertained. Little has been done, however, to meet this need. How meager is the information yet obtained

may be appreciated from the fact that Ford, in a 22-page discussion of the genetics of mimicry (see Carpenter and Ford), utilizes in the aggregate about a page and two-thirds to state the known facts. This includes statements of the progeny of females collected in nature after mating with unknown males; the actual experiments are very few. What information there is,

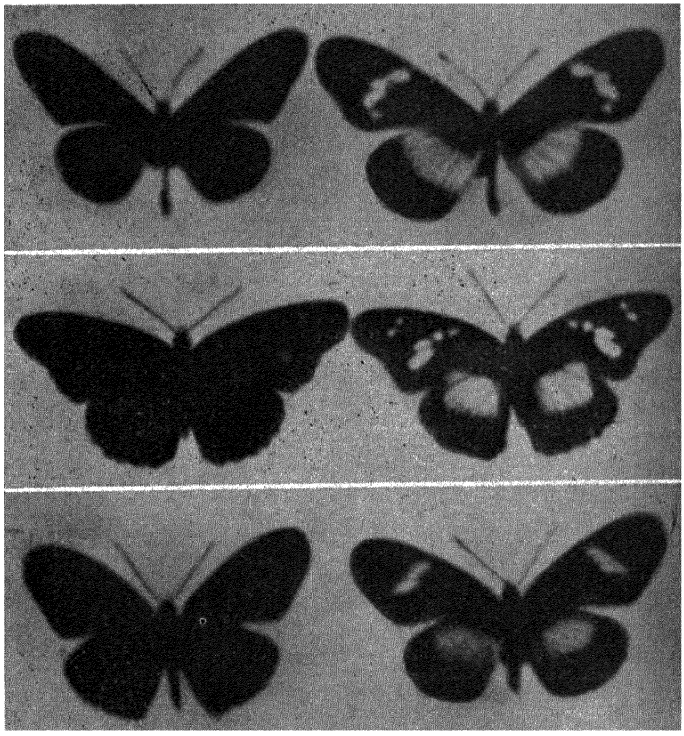


FIG. 49.—Mimicry extended to an invisible feature. The same butterflies as in Fig. 48, photographed by ultraviolet. The males (left) show as much similarity as by visible light. (*Courtesy of American Museum of Natural History.*)

however, goes to show that mimetic patterns are in general quite simple. They are due to only one or two gene differences. One of the most complicated instances is that of *Papilio polytes* studied by Fryer in Ceylon. This species has three races in the female sex, of which two are mimics of other species. The entire relation among them is controlled by two pairs of genes, both in some way modified by sex.

Now, the natural assumption based on these facts would be that mimics have arisen suddenly and full-fledged by one or two mutations. Under these circumstances there could be no long, gradual accumulation of the resemblance to the model. Natural selection could favor the mimicking mutant if its new character were really useful, but could have nothing to do with producing the similarity. There is still the possibility, which is pointed out by Ford, that many modifying genes have been involved in the process, and that in the accumulation of these modifiers natural selection has found a way to effect a gradual approach to the appearance of the model. However, since the simple crosses that have been made, in which modifiers would presumably be considerably dispersed, have still left the mimicking type plainly recognizable as such, it seems almost certain that most of the resemblance was attained by the first mutation. Much more extensive genetic work would be required to resolve these doubts, and it is to be hoped that the students of mimicry will proceed along that line of investigation.

Other Explanations of Resemblances between Species.—If mimicry has not arisen through selection of deceptive mutations, what other explanation may it have? It has several times been suggested that such similarity is mere coincidence. That view was held by the eminent entomologist Handlirsch. If one were able to classify insect patterns and colors by some objective unit, and set up some standard of similarity which would pass for mimicry, then it should be possible to calculate how often, among the 600,000 known insect species, similar patterns might have been arrived at by mere accident. Clearly the original classification of patterns could be valid only if based on a genetic analysis of them. This analysis is the crying need now, as has just been pointed out. It is not likely, however, that resolution of mimicking species into their genetic units would ever be used for such a classification and mathematical treatment; for in all probability many of the real phenomena involved in mimicry would then become clear without statistical handling.

Another suggestion is that mimicry may be the result of selection, but not through any effect on the visual apparatus of predators. Color must, like other qualities, have a physiological basis. Almost certainly color is not the only manifestation of that physiology. Probably no color or structure is

the sole result of the genes that produce it. If, now, it may be supposed that the color is due to a special physiology, that special metabolic activity may be of sufficient advantage to be preserved and increased through selection. Color would thus be purely incidental and itself of no use. A better knowledge of the development of organic pigments than now exists might reveal how different lines of descent could in this way acquire similar colors.

If it be assumed that similar colors and even combinations of colors may occur in different organisms purely as the result of physiological processes whose value is entirely divorced from external appearance, how, it may be asked, can we account for the arrangement of these colors in similar patterns in species not closely related? This is a problem of the development of the individual. If we knew how colors come to be arranged in approximately the same way in animals which *are* closely related, we might solve the problem of similar patterns in less closely related ones. Pattern is a phenomenon of development not yet understood. One important general result of the work on experimental embryology is the conclusion that cells do various things in an embryo, depending on where they are located. Situated at one place in the embryo, they do or become one thing; placed somewhere else, their activity or fate is entirely different. Why a change of position entails this change in the work of the cells is not known. Most geneticists have assumed that there is no fundamental difference or change in the cells, that is, that their genes are the same in any situation, and that only their response is changed. Wright, however, suggests that the genes may not remain the same. He thinks they may mutate as part of the developmental process. Mutations of genes in body cells are known to occur in various organisms, sometimes very freely. Wright has felt impelled to assume that such mutations occur in the genes governing pigmentation in mammals, and that where a spotted pattern is produced the genes mutate according to a gradient extending through the organism. That is, the mutations of color genes in somatic cells are governed by position. Spots occur in a certain place because, in that position, the physiological gradient decrees the appropriate mutation. The application of this idea to mimicry patterns should be clear in principle. The physiological

gradient need only be similar in those groups which have developed similar colors in order that the patterns may also be alike. It is to be remembered that, except in those faultily conceived instances of mimicry in which mimic and model are very close of kin, the patterns are not so much alike in detail that they can not be distinguished. It is as a rule only a general similarity of pattern that is attained, and it is not at all improbable that some principle of development may account for it.

Sexual Selection.—A third way of accounting for conspicuousness (warning color and mimicry being the other two) is through sexual selection. When one sex of a species is brilliantly colored, the other dull, the bright color was supposed by Darwin to be due to favor shown by the dull sex, and the idea has been taken up by many others. The species was originally dull in both sexes, but it is held that individual males mutated to somewhat brighter colors which aided them in winning the females. Such males would therefore leave more descendants to which their ornament would be transmitted. By repetition of such mutations and selection all males of the species would eventually be brightly colored. Examples are cited from many birds in which the males are conspicuous, the females dull; in fishes, especially during the breeding season when the males of many species become brightly colored; in lizards, many of which have colored patches on the head or on ridges of the skin; and in many butterflies, though these lower forms are suggested with more diffidence than are the vertebrates.

Any quality that might seem pleasing in the sight of the female ought to work similarly, and so there have been included, as results of sexual selection, ornaments of other sorts. The curious armatures of the staghorn and some other beetles which exist only in the male, the mane of the male lion, the crests and tail feathers of some male birds even if not colored, and the feathery tails of certain crustacea are examples. Courtship movements of the male ruffed grouse, turkey, peacock and lyrebird among birds, and of male fishes and male spiders are other presumptive ways of pleasing the females. So are the songs of male crickets, grasshoppers and cicadas.

Some emphasis has been put by supporters of the theory of sexual selection upon the color and behavior of the phalaropes. Contrary to the usual rule among birds, the female phalarope is

more brightly colored than the male. Moreover, in courtship she does the wooing; and in the domestic economy of the species the male incubates the eggs and cares for the young. The reversal of all the usual relationships simultaneously is thought to strengthen the theory.

By some, including Darwin himself who proposed the general theory, the weapons—spurs, antlers, horns, canines—by which the males fight one another for possession of the females are included among the results of sexual selection. Admittedly, however, this is a very different type of selection, and many biologists have preferred to think of it as simply one phase of ordinary natural selection.

The Question of Choice by the Female.—Proper working of the theory of sexual selection requires either that the males be more numerous than the females, or that they be polygamous, so that some males will not mate. In addition to this condition, there must be choice by the female, and concerning this there have been many opinions. Those who support the theory assume that she chooses among the males. That there is assortative mating in some animals has been proved, but it relates to size in most instances. In the protozoon Paramecium, in certain crustacea, and in some hermaphroditic marine mollusks individuals of about the same size pair. The reason is almost certainly mechanical, however, and does not involve choice by either sex. Choice is said to be quite evident in both sexes of the human race, and every individual who has passed the mating stage probably feels that he has exercised options; yet it would be very difficult for any one to say exactly what qualities had led to the selection, and his judgment would probably be in error if he did say. Moreover, the possession of the qualities commonly thought desirable appears not, at least in our present social order, to lead to more descendants. Animal breeders have pointed to what they call selective mating when two breeds of sheep, for example, have been mixed and each animal bred with others like it. Here, however, the selection is racial, and there is no evidence of selection among individuals. Even when a female is courted by more than one male there is no indication that she chooses among them.

More crucial evidence regarding mating behavior in one of the lower organisms, the promethea moth, was obtained by

Mayer in some experiments conducted on the Dry Tortugas Islands, far from the native home of the moths. By covering the antennae of the males with shellac he prevented them from finding the females, from which it was inferred that the female is ordinarily found by odor, since the antennae are known to bear the organs of smell. When some females were cut in two, the abdomen in one part, the wings, thorax and head in the other, the males came to the abdomen, but not to the wings, showing that the odor which guides them comes from the abdomen, and that they are not influenced by the wing pattern. When females were put into closed glass jars, the males did not find them, even though the females were clearly in view. It might be objected now that, since ultraviolet rays do not traverse ordinary glass, and since insects see in part by ultraviolet, the females in the glass jar did not look natural to the males. But if there was any doubt on this score, it was removed by Mayer's next step, which was to cut off the wings of some females, except the bases, and glue the wings of males to these stumps. Males mated with these male-appearing females as frequently as with others. Other males and females had their wings removed and nothing put in place of them, but matings occurred as before. Apparently the wing color or pattern has nothing to do with choice of consorts in these moths.

Other Objections to Sexual Selection.—One of the most frequently mentioned criticisms urged against sexual selection, aside from the lack of evidence for it, is the esthetic sense which it assumes the female to possess. There is no experimental evidence that the species in which conspicuous secondary sexual characters occur have an eye to beauty, to say nothing of their agreeing with us in their judgments. In view of this lack the observations of Selous on ruffs, birds related to the sandpipers, probably have little value. He watched the birds in their place of congregation for breeding, and saw that some males mated frequently, others not at all. The ones that mated were, in his opinion, among the handsomest. Whether the female birds agreed with him or whether their appearance was the cause of their frequent mating is uncertain.

Another criticism is that some brilliant males do not display their charms by any special courtship behavior. This would not be a fatal objection, since it might be only a tribute to the keen perceptions of a female which could reach a decision without

undue salesmanship. Still another objection is that courtship occurs in some of the salamanders in which the spermatozoa are not directly introduced by the male, but are attached in small masses to stalks of a jellylike material resting on solid objects. After the female is brought to the stage of sexual excitement she pinches off the masses of spermatozoa in her cloaca, but there is no certainty that she gets the spermatozoa of the male or males which courted her. A less forcible objection is that sexual selection assumes such a waste of energy on the part of males that any species which adopted that scheme would be wiped out by natural selection. These are samples of the many criticisms that have been voiced. For an exhaustive discussion of sexual selection the reader should consult T. H. Morgan's "Evolution and Adaptation." Such criticisms need not be further extended here in view of the other possible significance which sexual coloring and courtship have.

Other Proposed Meanings of Secondary Sexual Characters.—So far as courtship is concerned, its probable function is not to secure a mate but to arouse sexual excitement in her or even in the male himself. These two things may be quite different. A certain type of behavior may serve to create the degree of excitement necessary to the sexual act without beauty or any other quality of the male being at any time involved. Some experiments by Sturtevant on the vinegar fly Drosophila illustrate the difference between stimulating excitement and securing a mate. In this fly the male moves his wings in a characteristic manner when approaching a female as a prospective mate. It is a form of courtship behavior. Sturtevant clipped the wings off some of the males and found that they succeeded in mating, but that the act was long delayed as compared with normal males. He then put into a culture bottle with a female a normal male and a male with clipped wings. The clipped male mated almost as early as do normal males. The reason appeared to be that the normal male performed the usual wing movements, which helped incite the female to the mating act, and that once she had arrived at that stage she would accept any male. The exciting function of courtship had long before been suggested, but no such proof of it had been obtained.

Whether color in the male may help to excite the female is not clear. It is possible to maintain that it does, without much chance at present of confirming or refuting the argument. But

color may be quite incidental. Like other secondary sexual characters—behavior as well as structures—it is known to be due in a number of vertebrate animals to a chemical substance, a hormone, produced by the primary reproductive organs. Castration of a male when young prevents the development of the color or other secondary sexual characters, including ordinary sexual behavior. The hormone is thus necessary to the fundamental reproductive processes. It may well have been increased in effectiveness under the influence of natural selection. If another effect of the hormone is to produce color, or neck or tail feathers, or other ornament, that character may be entirely meaningless in itself. Such hormones have not been demonstrated in insects, so that secondary sexual characters in that group probably must have another explanation. But many sexual selectionists have shied away from insect examples on the ground that the esthetic sense and the power of choice are not likely to exist in a group with such low mental development—a group whose behavior is automatic in large degree. Julian Huxley has, however, endeavored to show that "choice" as involved in sexual selection may be automatic.

Wallace many years ago pointed out that the female, because of her importance in rearing the young, dare not be brightly colored, lest she reveal herself to predaceous animals. This consideration suggests that perhaps the natural course of evolution is for both sexes to become brilliant, but that owing to the repressive influence of natural selection the female has been forced to remain dull. That is, dullness, not bright colors, is the thing needing an explanation. This suggestion reminds one of Reighard's theory of immunity coloration proposed as a substitute for warning color. According to it inconspicuous color was induced by natural selection, in the face of a natural tendency to color, in species not in some way immune to attack.

CHAPTER XIII

DECLINE AND REVIVAL OF NATURAL SELECTION

> First of all, selection; that it does not operate in the form imagined by Darwin must certainly be taken as proved, but does it exist at all?
> ERIK NORDENSKIÖLD, 1928.

The theory of natural selection was not enthusiastically adopted by all biologists without question. There have always been objectors, and there are many at the present time. It is important in this connection not to confuse natural selection with evolution. Such confusion is common, and even some in high biological circles are or have been guilty of it. Darwin himself intertwines the two sufficiently to justify indiscrimination by others, for in his "Origin of Species" he not infrequently argues for evolution where the argument is supposed to be for natural selection. Numerous biologists later used the term Darwinism to mean evolution. Since evolution itself had been proposed and supported before Darwin's time, notably by Lamarck, the name Darwinism should be used to designate only Darwin's contribution to the doctrine. While Darwin proposed various theories, that relating to natural selection was the most important of them, and by common consent—with the exceptions just mentioned—it has received that name. Evolution was more readily accepted than was Darwin's proposed method of guiding it. Poulton comments that the meeting of the British Association for the Advancement of Science in 1881 was the last meeting of that body at which opposition to the doctrine of evolution was expressed. In the early years of the present century there was one European university biologist who disbelieved evolution, and at the present time a Scandinavian plant systematist who denies it. But such doubters are rare.

Early Opposition to Natural Selection.—Having thus clearly distinguished between opposition to evolution and opposition to natural selection, we may develop the latter more fully. Some of the more important criticisms leveled against natural selection

have been mentioned in an earlier chapter, and it only remains to indicate the times at which they have been urged. This may be done briefly, referring to only a few of the more important or more vigorous objectors.

"The Origin of Species" was published in 1859. In 1864 we find von Kölliker, an eminent Swiss anatomist and physiologist, then in middle age, convinced that natural selection was unable to do the things claimed for it. He accepted evolution, but suggested that in some way it had been brought about by considerable leaps, rather than by the slow accumulation of minute advantageous variations. Mivart, in 1871, urged the well-known objection that many structures of complex nature are useful only in a relatively perfected state, whereas, to be developed through natural selection, they must be useful from the beginning. Krönig in 1874 satirized natural selection by imagining trifling changes to have been made in industrial products with the idea of improving them, but with the actual result of ruining them. He held that these changes, directed by an (even though but slightly) intelligent being had a better chance of being advantageous than the purely accidental alterations with which natural selection had to work. Kramer in 1877 attempted to show mathematically that natural selection would not lead to the results it was supposed to produce, though it was largely sexual selection to which he specifically objected. Wallace supported sexual selection, doubtfully, it is true, in the eighteen-seventies, but opposed it in 1891. Nägeli, an eminent botanist, in 1884 developed seven criticisms of natural selection, including its reliance on accident, its claimed similarity to artificial selection, the usefulness of the beginning stages of complex organs, the failure of nutrition to produce heritage changes, the tendency of selection to render a species constant rather than variable, and its inability to explain the sharp gaps between species. Some of these objections were voiced by others later. Pfeffer in 1894 pointed out again the weakness of its dependence on accidental variation, and concluded also, curiously, that natural selection would act too speedily. He further denied the parallel assumed to exist between artificial and natural selection, since in the former the breeder uses only one character as a criterion, while in the latter it is the totality of characters that determines the fate of an individual. In the same year Ammon emphasized

another of Nägeli's points, namely, that natural selection would preserve uniformity instead of producing diversity.

Support of the Selection Doctrine.—To pursue these objections farther or to list them fully might give the erroneous impression that natural selection was given the cold shoulder by naturalists in general. Quite the opposite was true. In numbers and eminence its supporters may fairly be said to outweigh the opponents, even within only a few years after the publication

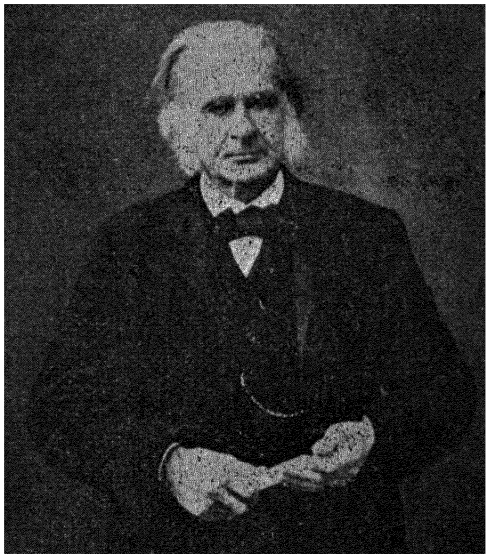


FIG. 50.—Thomas H. Huxley.

of "The Origin of Species." Only some of the more important advocates need be mentioned.

Prominent among Darwin's partisans was T. H. Huxley (Fig. 50) who sensed the need of an evolution doctrine before "The Origin" appeared. Huxley was particularly significant in the movement because of his early espousal of the cause in lectures, debates and popular articles. It was only a year after the publication of Darwin's epoch-making book that Huxley engaged in the famous debate with Bishop Wilberforce. Only another year later he made clear man's place in nature by ranging him along with the other animals. Huxley was much interested in paleontology and was impressed with the evidence for evolution found

in fossils. Darwin, it will be recalled, appeared to feel that paleontology was almost as much of a burden upon the theory as a pillar of support. Huxley had no such misgivings, saw in fossils much to confirm and nothing to refute the transformation idea, and in 1881 expressed his conviction by saying that if the evolution doctrine had not been ready at hand the paleontologists would have had to invent it. In all this vigorous campaign, however, it was chiefly evolution which Huxley championed, not natural selection. He sought a fair hearing for Darwin's doctrine, and is listed by Romanes among those who considered no other factor than natural selection necessary for the explanation of evolution. But Huxley made reservations, pointing out in particular that natural selection could rest more securely on artificial selection if the breeder had ever been able to induce sterility between any of his breeds derived from a common stock.

Wallace (Fig. 51) was another who supported the new theory with vigor. He was, indeed, coauthor of it. He went so far as to regard natural selection as *solely* responsible for evolutionary change. At first he favored sexual selection, but rejected it later because he regarded the distinctions supposed to have been developed by it as being really products of natural selection. Curiously, however, Wallace was unable to bring himself to include man, especially his psychological equipment, among the results of selection.

According to Romanes, Wallace was the first and for a time the only naturalist who held natural selection to be the only factor of evolution. He held this unique position up to the time of Darwin's death in 1882. Shortly thereafter he was joined by Weismann, and by a growing number of others under the influence of these two. Weismann developed a theory of heredity which involved a fixed and unchangeable "germ plasm" whose only evolution resulted from recombinations due to sexual reproduction. The ground was laid for this theory by his refutation of the then widely held theory of the inheritance of acquired characters. Admitting of no change from the outside, this germ plasm, for which a minute and complicated structure was invented, was subject only to a reassortment of its parts. From among these various rearrangements nature selected, and all evolution proceeded from this source. Weismann was obliged to alter his conceptions in later years to fit a number of phenom-

ena, but in the period before 1890 his influence was strictly on the side of an evolution completely controlled by natural selection. Romanes called this advocacy of natural selection and that alone, by Wallace and Weismann, "out-Darwining Darwin." Darwin, it will be remembered, had never given up

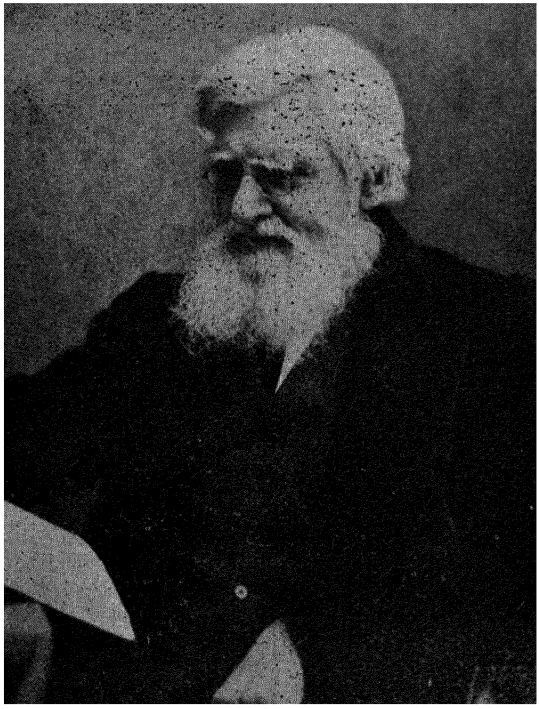


FIG. 51.—Alfred Russel Wallace. (*From Wallace, My Life, Chapman & Hall.*)

inheritance of acquired characters. He had invented the theory of pangenesis according to which the germ cells collected representative bodies, the gemmules, from the body cells, and were therefore in a position to transmit somatic modifications to the next generation. Romanes strongly championed the Darwinian doctrines, and regarded himself at one time (about 1893) as the only real adherent of Darwinism. Other naturalists were classified as neo-Darwinians, those who recognized only natural selection, and neo-Lamarckians, those who gave inheritance of acquired characters a more important place than Darwin did.

It may be suspected that Romanes insisted on Darwinism as Darwin had developed it more for the sake of inheritance of acquired characters which Darwin accepted than because of his natural selection. All in all, Romanes estimated that all naturalists within a decade after Darwin's death included natural selection as part of their theories of evolution, and that they differed only as to whether there were also other factors, and the relative importance of these factors.

In Germany, the first biologist to espouse the cause of evolution wholeheartedly was Haeckel, who preceded Weismann in a decisive announcement of that adherence by nearly two decades. But Haeckel had little to say regarding natural selection. He was interested in family trees, not factors, and is probably best known for his support of the "biogenetic law" according to which each individual in its own development recounts the history of the race. In America the most vocal of the evolutionists were the neo-Lamarckians, mostly paleontologists, led by Cope, who stressed the inheritance of acquired characters, though presumably also admitting an influence of selection. Among other American biologists it is the testimony of some still living that natural selection was generally recognized as one of the factors of evolution.

Reaction against Natural Selection.—It is thus apparent that at the time to which this account has been brought, the early years of the last decade of the nineteenth century, a third of a century after the publication of "The Origin of Species," the doctrine of natural selection had won general though not complete acceptance. Romanes was at that time so enthusiastic over the progress of the theory that he predicted another ten years would witness the solution of all outstanding problems and general agreement regarding the method of evolution.

Even at that time, however, the basis was being laid for a reaction against natural selection which extended over the end of the century—a reaction which never affected all naturalists, but which involved a number of the most eminent biologists of America and Europe. While most biologists were ready to accept selection as a principle in nature, they were unable to follow the many proponents of the doctrine in their applications of it. Even some of the ardent supporters of selection, like Wallace, could not accept sexual selection. There were even

more who doubted warning color, mimicry and signal colors. The alleged examples of the results of these special forms of selection seemed to many biologists so improbable that the method in general was rejected. It was not easy to differentiate between these special kinds of selection and selection as a general principle. Consequently there arose doubt as to the validity of the fundamental rule itself. This is the fate of nearly every new generalization, it is quickly applied to many phenomena with which it has nothing to do, and doubt as to its verity anywhere is engendered.

Influence of the Mutation Theory.—So long as the objections to natural selection were based only on its inability to do the things claimed for it, they made no marked headway. For some curious reason most people do not readily reject a doctrine unless there is another to take its place. So far no promising substitute was in sight. Then, however, came the mutation theory of De Vries. This Dutch biologist (Fig. 52) had witnessed in the evening primrose Oenothera the production of many offspring which differed from their parents in certain well defined characteristics. Similar though smaller changes were soon observed in other organisms. The modifications arose without any apparent cause and persisted in subsequent generations because they were inherited. These are the changes with which we have already become familiar as mutations.

Biologists early began to see in mutations a means of originating new species. Since the changes were full-fledged and some of them quite marked at the outset, and since they were at once permanent and did not increase in subsequent generations, selection seemed not to be necessary. For natural selection had been thought of as accumulating numerous scarcely perceptible variations, and hence as resulting in gradual change. The new mutations were not gradual, they arose complete at one step and did not grow thereafter.

It is a little unfortunate in this connection that the first mutations to attract attention were those of Oenothera. These were mostly sizable changes affecting a number of parts of the plant. The differences between a mutant plant and its parent were often quite as extensive as the differences between two species of the same genus in other organisms. De Vries for that reason called them "elementary species," indicating his own opinion

that new species had arisen at a single step. Probably their size was the reason why these changes in Oenothera were the first ones seen. Had they been smaller, such as the omission of

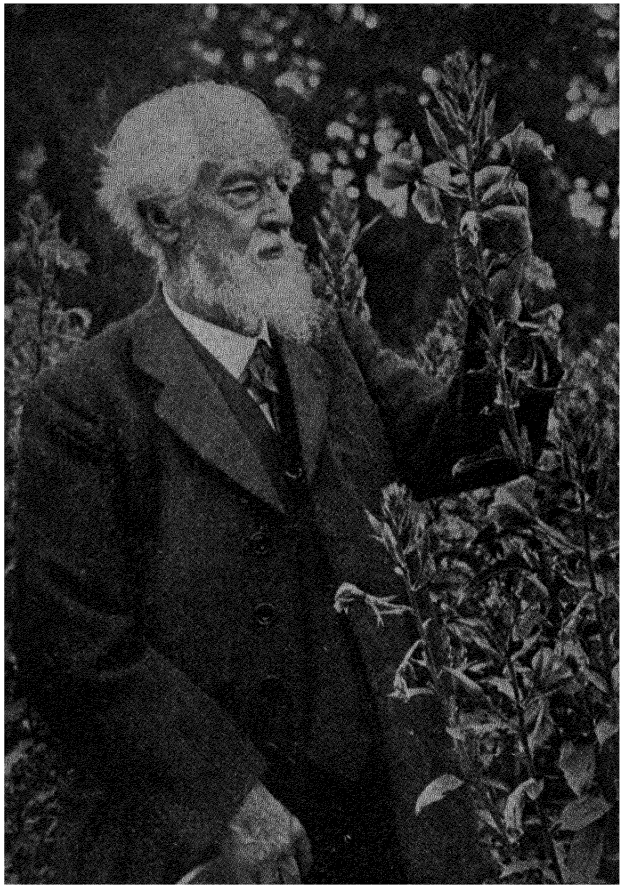


FIG. 52.—Hugo DeVries. (*From Journal of Heredity.*)

several of the strong spines of the vinegar fly, it is not likely they would have been so readily discovered; and had they been discovered despite their insignificance they would not have suggested at once that a new species had come into existence. The changes in Oenothera have since been shown to be largely of a sort which

should probably not be called mutations. Most of them are not changes of single genes, but are modifications of chromosome groupings. Chromosomes joined end to end form rings of various sizes in the several kinds of Oenothera, and the "mutations" of De Vries were many of them alterations in the composition of these rings. Such rings are not common in other organisms, and so the changes observed in Oenothera are not to be duplicated everywhere in the living world. Nevertheless, the idea that species could originate fully formed at a single step was carried over from the evening primroses to other organisms whose mutations are changes in single genes. Thus came about the notion that the occurrence of mutations made natural selection unnecessary. One of the best expressions of this view is found in Morgan's "Evolution and Adaptation," published in 1903, in which natural selection was subjected to vigorous attack from many angles.

Negative Results of Selection Experiments.—It was in an evolutionary atmosphere of the sort just described that Johannsen published (1903) the results of some selection experiments with beans. In these experiments it was demonstrated that an ordinary field of beans is a mixture of races having somewhat different characteristics. The size of the beans may be used to illustrate these differences. While the size of the beans of any one race fluctuates considerably, so that the races overlap, each race has a mean size about which its members are distributed, and this mean size may be quite different from that of another race. Now, when large beans are selected out of an ordinary field for planting, they naturally come mostly from the larger races, and the beans of the next season average larger. Selection of large beans for planting again the next year restricts still further the number of larger races which are drawn upon for propagation, and a further increase in size of the progeny results. But Johannsen's experiments dealt primarily with selection within a single one of these races. Starting with a single plant, which was allowed to self-fertilize as beans normally do, he was assured of having a single race, which he called a pure line. As explained above, the beans fluctuate in size even within one pure line, so that selection of large beans for planting could be practiced here as well as in a mixed field. However, after a number of generations of selection for large size on the one hand, and for

small size on the other, the mean size of the beans had not been altered in the least.

A few years later Jennings (1908) performed some comparable experiments with the protozoon Paramecium, an organism which reproduces asexually by simply dividing in two. When selection for large or small size was carried out in a mixed lot of paramecia collected in nature, the mean size was shifted in the direction of selection. But when the selection was done within a single race of paramecia (that is, among the descendants of one single animal), no such change was effected. Selection was again effective when it was practiced on a mixture of races, which were thus sorted out from one another, but was ineffective within a single race.

At the time, these experiments were interpreted by most biologists as against the Darwinian doctrine. In the light of present knowledge it is clear that they do not oppose that doctrine, but speak strongly for it. Yet it is not difficult to see why the general impression then was the reverse of this. In the first place, mutations were still new. No one had explored their possibilities. No one had seriously considered the question whether they could of themselves, without aid from any other process, really initiate new species. Secondly, from the beginning natural selection had been supposed to seize upon minute fluctuations, and accumulate them if they were useful. While Darwin knew that some modifications are inherited, others not, neither he nor any one else regarded these alterations as belonging to two fundamentally distinct classes. Today we recognize the inherited ones as being due to changes in the germinal material, the genes, or at least in the chromosomes or some other transmissible entity, while the uninherited ones are due to environment in a broad sense. Even in the opening years of the present century most biologists did not clearly perceive the distinctness of these two categories. When therefore, fluctuations occurred within a pure line of beans, or in a single race of paramecia, it was generally held that these were the things upon which selection was supposed to operate effectively. When selection produced no effect, this result was held to contradict the Darwinian theory. These fluctuations are, of course, the environmentally produced ones, they do not rest on germinal changes. Had biologists then looked away from the unsuccessful

selection within a race, and observed the success of selection performed on a mixture of races, they should have seen what it is that selection can do and what it has no power to do. But it takes time for ideas to germinate and take root.

These selection experiments had the general effect of accentuating the reaction against natural selection. It must not be understood, however, that biologists were ready to cast natural selection wholly aside, even at the low point of this reaction. Some doubtless were, but many, perhaps most, recognized that it might stand as a valid principle if we only knew how to use it. Kellogg's "Darwinism Today," published in 1907, marshals the evidence for and against selection much as a convinced anti-Darwinian might do, but in the end expresses the view that in some manner perhaps not yet understood the selection theory *must* work.

The Effect of Mendelian Theory.—Though Mendel's principles were rediscovered in the year 1900, and though every evolutionist from Darwin on—and none more than Darwin—recognized the important relation existing between heredity and evolution, no appreciable influence of Mendelian theory upon evolutionary speculation was discernible in the early years of the present century. Kellogg's book, referred to above, mentions Mendel (Fig. 53) briefly, but uses his work only to reinforce what is said regarding mutations, which might have been based solely on the work of De Vries done during the ten years before Mendel was rediscovered. That is not surprising, for Mendelian heredity was not yet understood then. It required twenty years to get even a moderately clear view of the mechanism whose more elementary fundaments Mendel had postulated, and it required another ten years to acquire certain of the details which mean most for evolution.

Expressions of surprise have sometimes been called forth by the failure of evolutionary writers to make more use of Mendelian phenomena during this period. Every general treatise on evolution included its chapter or chapters on heredity, in which the Mendelian scheme was described, and in which the obvious connection between heredity and evolution was pointed out. But not one of these treatises made any attempt to show precisely how evolution must take place, in the light of this relation. Perhaps this tardiness is reprehensible. More likely, however,

it is a boon to future generations of biologists. For, had detailed consideration of the method of evolution as dependent on the heredity mechanism occurred while that mechanism was less perfectly understood, it would almost certainly have been riddled with serious error. Probably all of it would have had to be done over, with greater difficulty for having been done once, differ-



FIG. 53.—Gregor Mendel. (*From Genetics.*)

ently, before. Indeed, it would not be difficult to make a strong case for the assertion that evolution doctrine as a whole would be sounder today if all speculation concerning it had been banned between the publication of "The Origin of Species" and the second or third decade of the present century. The chief possible error in such a statement is that evolution speculation might have helped stimulate the discovery of mutations and Mendel's laws, but it is not at all clear that it exercised any such stimulus.

The Revival of Natural Selection.—Just how, or when, natural selection began to be again more favorably regarded can not be

stated. It was a gradual process, involving a change in the attitude of many biologists. To what extent its revival has already occurred it is likewise impossible to say. Such movements can not be measured. When, in 1916, Castle and Phillips demonstrated the effectiveness of selection in hooded rats, where genetic differences and not merely fluctuating environmental effects were concerned, a glimpse of the possibilities of natural selection was again caught. One investigation does not, however, change the whole trend of thought, and as late as 1930 Pearl pointed out how little experimental evidence of the effectiveness of natural selection had ever been obtained. He showed that the results which must follow natural selection, step by step, in order to produce evolution had never been proved to occur. This did not mean, of course, that natural selection had not so operated. If only those things were true which have been proven true, there would be little verity in the world. It may merely have meant that proof of the effectiveness of natural selection was a labor so great that no one had performed it.

Increasing knowledge of the details of the genetic mechanism, its genes and their mutations and interactions, its fortuitous recombinations and chromosome aberrations, and its meiotic control of recombinations gradually formed a basis upon which a new interpretation of evolutionary phenomena can be based. It is along this line that the newest developments have occurred in the hands of Wright, Fisher and Haldane, and here the greatest promise for the immediate future seems to lie. These investigators have considered the purely random behavior of genes, using the mathematics of chance as a tool. They have thus determined what course the changes in the gene composition of a population might take if not influenced by any outside agency. To this they have added, singly and in combination, the effect of migration into and out of the population of individuals possessing other gene combinations, the consequence of repeated mutation of the genes in the same way, and the result of any advantage or disadvantage conferred on individuals by a gene or combination of genes. Some of their simplest conclusions have already been presented; most of them are too complex for treatment here. Their efforts represent the first attempt to apply mathematics to the problems of evolution in the light of modern knowledge of the genetic mechanism. The results are promising, and furnish

at present the best outlook for the development of evolutionary thought of the future. There is not entire agreement among these biologists as to when and how natural selection begins to work. Fisher holds that it begins as soon as the effect of a new gene manifests itself, and that nothing else is of comparable significance at any stage of evolution. Wright, on the contrary, conceives that races may come into existence largely through the accidents of recombination and migration, and that selection first operates effectively upon these races. But they agree that selection is eventually the most powerful of all the directive agencies.

And so the theory of natural selection is coming back. Perhaps one should say that it has returned. But it gives signs of being a different doctrine. Life-and-death value of certain characteristics to their possessors seems no longer so important. The leaving of many descendants is recognized as the criterion of success, and there are other ways of assuring the permanence of one type besides killing off its competitors. The struggle for existence need not occur in the form of a competition. There may really be some plain accident in the fate of classes of organisms. And above all there is some indication that the myriads of minute and particular characteristics which were once thought of sufficient importance to animals to insure their own perpetuation will no longer be regarded as supreme. If the doctrine can emerge minus its sexual selection, its warning colors, its mimicry and its signal colors, the reaction over the end of the century will have been a distinct advantage. These special forms of the selection idea may persist in spots owing to the prestige of their sponsors, but they seem destined to be dropped, or at least relegated to very minor places in evolution discussion.

CHAPTER XIV

ISOLATION IN THE FORMATION OF SPECIES

> It becomes apparent that the transformation of a mutant race into a species must ordinarily depend upon some sort of isolating factor which will prevent its interbreeding with closely related stocks.
>
> A. C. KINSEY, 1929.

It has long been the opinion of many biologists that isolation of groups of individuals from one another has played an important part in the origin of species. The first ardent proponent of isolation in evolution was Moritz Wagner, who began a series of articles in its support in 1868. He did not in his own lifetime have the satisfaction of seeing his theory adopted by many naturalists, but since that time his view has been adopted by most systematic biologists—those interested primarily in classification—especially the systematists interested in geographic distribution as many of them are.

Geographic Isolation.—The isolation which was first appealed to was geographic separation of groups, as is indicated by the stress which Wagner placed on his "law of migration." Whatever the cause of spread may be, all species tend to occupy greater and greater areas if they are not stopped by barriers. It goes without saying that as a result of this migration groups of individuals find themselves in different localities. Such differences were not supposed to have any effect in evolution, however, unless the separation prevented or reduced crossing between the groups, thus resulting in inbreeding within each group. It is worth while to discover whether, to what extent, and how this effect is produced, and what influence it has on differentiation of species.

It is obvious that if any portion of a species exists on an island while the rest of it is on the mainland, and members of the species cannot, or can only rarely, cross the water barrier between, the isolation described above is attained. If different mutations should arise on the island and the mainland, or if the same

mutations arose and different ones were fortunate enough to pass the stage of accidental early preservation in the two locations, the two portions of the population would come to differ. An even more marked result would follow if conditions were somewhat different on the two land bodies, so that natural selection led to different developments in the two populations. Island faunas are well enough known, and differ sufficiently from those of other islands or the nearest mainlands, to indicate that such differentiation does accompany isolation. Examples are given in the account of geographic distribution in an early chapter.

Most species, however, are not so completely, or at least so obviously, separated from the most nearly related other species. While very closely related species do not usually occupy much territory in common, they are nevertheless not far apart. They are in fact usually side by side. How do they acquire these neighboring positions? If they have come, as supposed, from a common stock quite recently, their origins must be looked for in an undivided species. When members of a species migrate, as all of them do, they come to be widely separated. Individuals on the borders of the range may be hundreds or even thousands of miles apart. Without extraordinary powers of migration these distant individuals are just as effectually prevented from interbreeding as if they were separated by a channel of water. Moreover, isolation is much more marked than these figures indicate, for hundreds of miles are not needed. We have already seen, in considering the phenomenon of "territory" (page 142), that migration by individuals may be very slight indeed. A mouse in one season usually covers only several acres. It appears to regard this small area as its own by squatter sovereignty, which it maintains if necessary by fighting; and it no doubt expects to have its incursions into other areas resisted in the same way. Birds are known to cover a larger area, but in relation to their means of locomotion the extent of their travels is small—a square mile or less in small species. Many birds migrate seasonally, but since they do not breed during their travels, and since many of them seem to return to the same spot year after year to nest, they still occupy only limited areas at the time when crossing might occur. Most animals must be restricted to mating with other individuals quite near them. Consequently there is in any one generation as much isolation of

groups separated by a hundred miles on land as there would be if one of them were on an island, the other on the mainland, with a hundred-mile-wide channel between. The only difference between the two relations is that, after many generations, the descendants of the two separated groups on land may begin to meet, while descendants of those separated by water are still kept apart. If those many generations are enough to bring about shifting of gene ratios and accumulation of different mutations in two groups, the isolation on land is quite as effective and of precisely the same kind as separation by water.

Restriction of Hybridization.—The shifting of gene ratios and accumulation of different mutations are not adequate, however, to produce the known differences between most species. Any closely allied species which have any opportunity to meet, as they commonly do on land and in the absence of other barriers, should, if shifting of gene combinations and accumulations of the mutations that make them visibly different from one another were all that occurred, hybridize with one another. It is important to understand what would result from hybridization if it occurred freely. Early evolution writers almost without exception assumed that new mutations (they were not called mutations then) as they arose in a species would be "swamped" by crossing with nonmutant individuals. It was the supposed function of isolation to prevent this swamping. Unfortunately this same fate has been assigned to them by some much more recent authors. Now, no gene is ever swamped (lost) by hybridization. Genes are lost only by the loss of the individuals or the germ cells possessing them. They exist in the hybrids just as in one of the parent types. Instead of swamping genes, hybridization may be quite as well regarded as introducing genes into other stocks. Crossing is a leveling, not a destroying influence, and the leveling may be upward as well as downward. It may increase the prevalence of a gene in new stocks, rather than suppress it in an old one.

Consequently, species arising in situations where crossing is not prevented would almost necessarily be connected with one another by many individuals possessing some genes of each group. In like manner, if two species previously in entirely separated areas should sometime meet and hybridize, their hybrids should contain some genes of each. On the whole, in

either of these instances no matter what dominance or lack of dominance existed between the contrasted genes, such hybrid individuals should be more or less intermediate between or composites of the two contributing types. But, as was pointed out in the first chapter, species are not as a rule connected by many intermediate individuals. While a few such intermediates may be found, they are much less numerous than would be expected from the ordinary operations of hybridization if crossing can occur freely. Species are therefore usually rather sharply defined.

From this sharpness of specific distinctions it might have been, and was, inferred that crossing between species is uncommon. Moreover, as attempts to hybridize species were gradually made by practical breeders and others it was found that a considerable restriction upon the process does exist. A small number of instances of free interbreeding of species are known, and biologists sometimes comment upon the fact that there are so many of them; yet compared with those that do not cross at all or do so only feebly the number of readily hybridizing pairs of species is unimportant.

Degrees of Crossability.—When species hybridization is possible it occurs with varying degrees. Plants have yielded more successes than animals. Within one section of the genus to which the snapdragons belong, the species cross freely with one another, but these species do not cross at all with the species belonging to another section of the same genus. In the plant Crepis two of the species cross readily with one another, but two other species only with difficulty. Most ordinary tobacco strains may be crossed with a certain wild species of the same genus (Nicotiana) and yield about 1 per cent of a crop of good seed; but one particular variety of tobacco ("Cuba") crosses with the same wild species producing a full yield. In animals, the species of the fly Drosophila cannot as a rule be crossed, but *D. melanogaster* and *D. simulans*, the most similar of all the species, can be hybridized.

In some animals and plants crosses between different genera are possible. Probably the most general of these are among the pheasants, for the gold pheasant has been crossed with the hunting and the silver pheasant, and the latter crosses with the ring pheasant. Sometimes the heterogeneric crosses are

one-sided, for wheat may be pollinated by rye, but not rye by wheat; and the radish may be pollinated by cabbage, but not cabbage by the radish.

Infertility of Species Hybrids.—Whether two species or two genera will cross is not, however, the only question of evolutionary importance. It is of quite as much moment whether their hybrids can breed. Here again there is a wide range of situations. The snapdragon hybrids are fully fertile; but the radish-cabbage hybrid is mostly sterile. Hybrids between Nicotiana (tobacco) species may produce over a thousand good seeds per capsule, or less than a dozen, depending on the species used. Mules, which are hybrids between the horse and the ass, are nearly, though not quite, always sterile. Fertility of hybrids is sometimes bound up with their sex. Thus the domestic cow may be crossed with the bison (an intergeneric cross), producing somewhat fertile females, but sterile males. The hybrid between two species of Drosophila, mentioned above, is completely sterile.

Since success in evolution depends on numbers, it makes little difference when the incompatibility of distinct taxonomic units appears. If species hybrids are produced, even abundantly, only to prove sterile or of greatly reduced fertility, evolution is not likely to be affected much more than if the species could not be crossed in the first place. It is this sterility of hybrids that maintains the sharp distinction, the rarity of intergrading individuals, between allied species.

Obstacles to Specific Crossing.—What are the sources of this infertility of species with one another? Important inferences concerning evolution depend on the answer to this question. In plants, the chief obstacle to crossing is the fact that the pollen tube must grow through the style and other tissues to reach the egg, and it does not find the tissues of a foreign species suitable soil. In animals, psychological features may prevent mating. Odor of one or both sexes is known to be a means of bringing the sexes together in some insects, and probably serves as a sexual excitant in many animals. If a foreign species lacks this odor, even the first step toward hybridization is not attempted. In the older literature of isolation morphological reasons were often assigned for the failure of species to cross. Thus, in some insects the form of the male genitalia was held to be unsuited to the

apposite parts of the female. In most such instances, however, it was not definitely shown that the difference in structure did really preclude copulation; and in some species the shape of the genitalia could not be important, since the male genitalia of a group of species of craneflies are quite different while the cor-

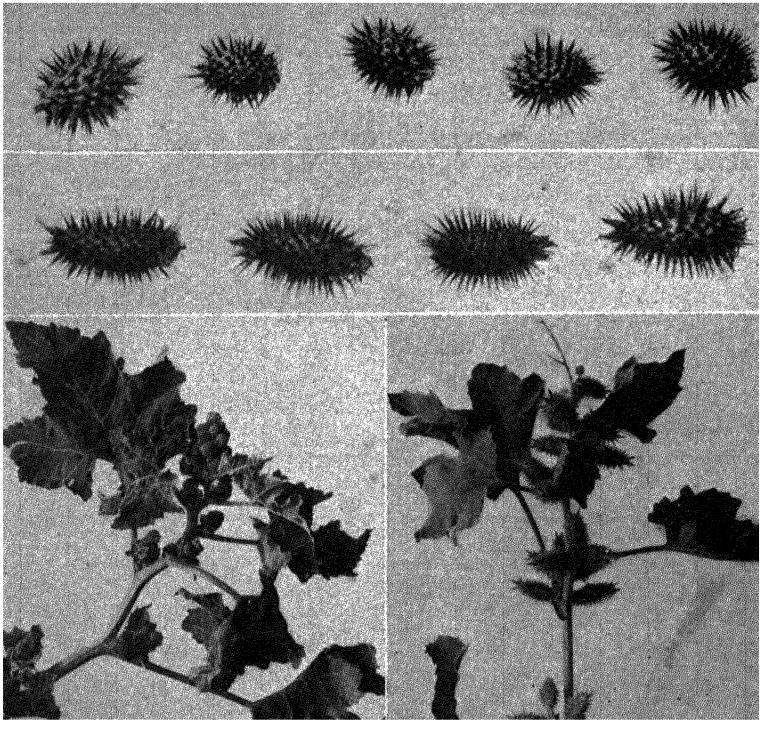


FIG. 54.—Species isolated by different times of maturity of their germ cells. Top row and lower left, *Xanthium globosum*, whose flowers open after seed capsules of *X. pennsylvanicum*, second row and lower right, are fully formed. (*From C. A. Shull, in Botanical Gazette.*)

responding parts of the respective females are practically identical, indicating that the shape of the male genitalia has no functional significance. It has been said also that right- and left-coiled snails find copulation difficult. Other possible ways of preventing species from crossing are having the mating instincts and the germ cells develop at different times of the year (a condition existing in two types of cocklebur, Fig. 54, and reported to hold even for two varieties of a certain species of

shore bird), chemical or physical differences of eggs and spermatozoa which make union of these cells from different species difficult or impossible (certainly known for very few closely related species), and subtle psychological properties other than smell, which has already been mentioned, such as "race-feeling," concerning which there is no certain knowledge.

Correspondence of Chromosome Numbers in Hybrids.—When species do cross, the relative sterility of their hybrids which usually obtains may rest on a variety of causes. If the hybridizing species have different chromosome numbers, the chromosomes can not usually be arranged in homologous pairs. If a species having 18 chromosomes is crossed with one having 10, the hybrid should have 14, of which 9 came from the former parent, 5 from the latter. Ordinarily these 14 chromosomes do not constitute 7 homologous pairs, hence the pairing of the chromosomes before meiosis does not take place, or is only partial. Some or all of the chromosomes are left unpaired, and the distribution of the chromosomes to the germ cells is irregular. This irregularity of the chromosome content may not be fatal to the germ cells, but is usually fatal to the individuals which should develop from the fertilized eggs. Only occasionally, if ever, do two germ cells of such hybrids uniting in fertilization possess the right chromosomes to make a viable individual; thus a high degree of sterility results. In the sundews one species has 40 chromosomes (germ cells 20), another species 20 (germ cells 10). Their hybrid has the expected 30, but these do not form 15 pairs. Ten pairs are formed, involving all 10 of the chromosomes from the 20-chromosome parent and 10 of those from the 40-chromosome species, while the other 10 from the 40-chromosome species remain single. In the meiotic division the 10 pairs behave regularly, one member of each pair going to each cell, but the 10 unpaired chromosomes are distributed irregularly. As a consequence, few or none of the germ cells have a suitable set of chromosomes, and the hybrid is sterile.

The severity of this stricture against species crossing is mitigated somewhat when one of the species has been derived from the other by a doubling or other multiplication of its chromosomes, or when both have been produced by different multiplications of the chromosomes of a third species. Thus wheat has 42 chromosomes, and emmer has 28, but it is believed that both

have come from a species having 14 chromosomes. When wheat and emmer are crossed, the hybrid receives 21 chromosomes from the former and 14 from the latter. In the hybrid, 14 pairs of chromosomes are found undergoing meiosis, while the other 7 act irregularly (Fig. 55). Since the 14 pairs include a double set, as compared with the original 7-pair species from which wheat and emmer both arose, the hybrid is quite successful. The seven irregular chromosomes, or most of them, may be absent from some of the germ cells of the hybrid, and these produce normal, or nearly normal, offspring. Other species

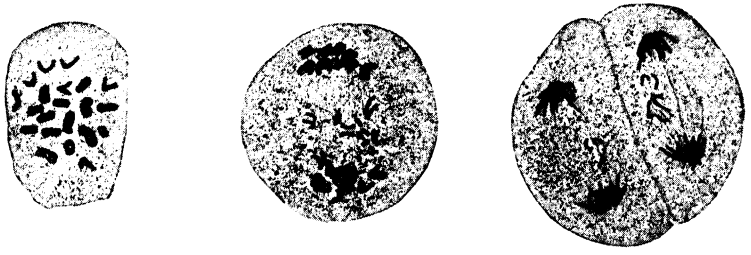


FIG. 55.—Meiosis in hybrid of emmer and wheat. Cell at left has 14 pairs of nearly homologous chromosomes, and 7 single ones which may be nearly homologous with those of the pairs but have no mates. These 7 behave irregularly in the divisions. (*From Sinnott and Dunn, Principles of Genetics, McGraw-Hill Book Company, Inc., after Sax.*)

may tolerate the extra chromosomes and produce offspring despite the irregularities.

Within species whose chromosomes are multiples of other species there is some reduction of fertility. In those having the $4n$ number, fertility is reduced only moderately. In *Oenothera gigas*, for example, there are four chromosomes of a kind, and these chromosomes assemble in groups of four, instead of in pairs, prior to meiosis. If in the meiotic division the four chromosomes were always assorted two and two to the cells, there should be no appreciable disturbance in the processes that follow; but occasionally they separate three and one, and abnormal eggs and pollen are produced. Enough irregularities of this kind occur to reduce the fertility about one-fourth. In forms having the $3n$ chromosome group, irregularities are common. The chromosomes collect in groups of three before meiosis, and it is impossible to assort them equally to the two cells in the meiotic division. A certain small number of germ

lls receive one chromosome of each group, or two of each group, ıd these are functional. In some such species, a little more lerant than others, germ cells are functional even if they hibit slight irregularities in their chromosome content, and these the fertility is correspondingly higher. Questions of rtility within species do not, however, bear on the phenomenon isolation.

Confused chromosome situations are well known in hybrids of bacco, wheat and other plants. Many of the species of ımals whose hybrids are sterile also have different chromosome ımbers, and enough is known of the cytology of the hybrids some of them to indicate that inability to match the chromomes of the two original species is at least part of the cause of the ɜrility. The chromosome behavior is of so many kinds, hower, that it is impractical to make any generalizations. Somenes the hybrids of one sex are fertile, those of the other sex ɜrile. Thus the hybrid of the domestic cow with the bison fertile if female, sterile if male. The reason is not, however, ıderstood.

Homology of Genes in the Chromosomes of Hybrids.—While any crossable species differ in their chromosome numbers, and ıile this difference could account for sterility of their hybrids, ere is much to indicate that mere number is not all that is ıportant. It is necessary that the chromosomes coming from fferent parents should pair before meiosis in order to insure at each germ cell will get one chromosome of each kind. ıromosomes do not pair with just any other chromosome, they ,ir only with other chromosomes much like themselves. That the pairing chromosomes must contain, to some extent at ıst, similar genes (see Fig. 56). How the homologous genes tract one another is not known, and there are known examples pairing chromosomes which differ in a considerable number of eir genes. Nevertheless, the general rule stands that homology the genes favors the pairing of the chromosomes in which the nilar genes reside, and that chromosomes not in any way ımologous do not pair. Consequently, unless two species e very much alike, their chromosomes may be so different at no pairing occurs in their hybrids. The numbers of chromomes may even be identical, and yet they do not pair. The ndews mentioned earlier work as they do because, notwith-

standing different numbers of chromosomes, there is still a great deal of similarity of the ten chromosomes of one species to 10 of the 20 chromosomes of the other species.

Since correspondence of many genes in the chromosomes is necessary to pairing of these chromosomes, there are clearly other ways of disturbing this process. The chromosomes may become attached to one another in various ways. Thus in the vinegar fly *Drosophila melanogaster* the so-called X chromosomes, which are associated with sex, are straight and rodlike in form. In *Drosophila willistoni* there are also straight rodlike chromosomes, but these are not associated with sex; the sex chromosomes are much longer and bent. This may be explained by assuming that the X chromosomes in *D. willistoni* have become attached to the ends of other chromosomes, or perhaps only fractions of

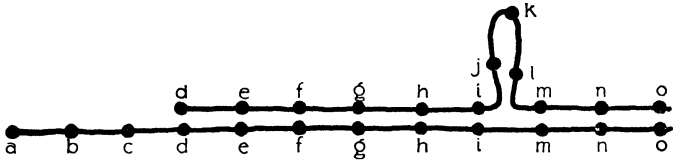


FIG. 56.—Pairing of two chromosomes whose genes are only partly similar, illustrating how the corresponding genes pair notwithstanding their different positions in the chromosomes.

other chromosomes. It is not possible to cross these two species of Drosophila, but if it were the reorganization of the chromosomes might be expected to interfere with meiosis and so cause reduced fertility in the hybrid.

Rearrangements within Chromosomes.—Inversions may cause difficulty in the pairing of chromosomes. The best known case of inversion in nature is that exhibited by two species of Drosophila, *D. melanogaster* and *D. simulans*. These species are more alike than are the other species of the genus; are so similar, in fact, that they were not recognized as separate species until sterility of their hybrids was discovered. Fortunately they can be crossed; and still more fortunately corresponding mutations—many of them— have arisen in both species. Crossing of the species has made it possible to demonstrate that these mutations, which are recessive, really are identical, for only if they were identical would the hybrid ever show the same mutant characters. So it has been possible to determine the position

of many of the same genes in both species; that is, maps of the chromosomes, involving identical units, have been prepared for both species. One of the chromosomes of *D. melanogaster* corresponds, gene for gene so far as the mutations permit their detection, with one of the chromosomes of *D. simulans*. The order of their arrangement is the same, though the apparent distances between them are slightly different. The striking comparison of the two species is that one other chromosome of *D. melanogaster* corresponds to one of *D. simulans*, except that a segment of considerable size in the middle of the chromosome is turned end for end. The mutant genes in that section run peach-aristipedia-delta-hairless in one species, but hairless-delta-aristipedia-peach in the other. In the hybrids these chromosomes would have similar genes, but like genes would not be side by side in the middle region of the paired chromosomes except through a looping or some other peculiarity of position of the chromosomes (Fig. 32, page 95). How much difficulty this lack of correspondence would create is not known. The hybrids are sterile, and their sterility has frequently been attributed to this inversion. Against this explanation, however, is the fact that the reproductive organs of the hybrid are degenerate, and that the degeneracy is obvious before the stage at which homologous chromosomes would begin to pair. There must be some other reason therefore for the sterility of the hybrids between these particular species. This does not necessarily mean that inversion is never a cause of sterility. The lack of correspondence of the genes which extensive inversions bring about should theoretically cause difficulties in meiosis, and sterility may in some instances be a consequence, even though no such case is known. Since no other species differing chiefly by the inversion of a chromosome segment are known, the possibilities of interspecific sterility as a result of such rearrangement of genes can hardly be said to have been explored.

Other Chromosomal Modifications.—The other chromosome aberrations are likewise possibilities without any actually known examples in nature. Deletions, or the absence of portions of chromosomes, may conceivably cause intersterility. They may not be a very common source of difference between species in the first place, because the mere loss of portion of a chromosome would probably be fatal when such a defect was present in both

chromosomes of a homologous pair, as it would have to be to make a true-breeding species. But if the genes omitted in a deletion could be replaced by an extra chromosome of that kind, or an extra piece of chromosome containing them placed somewhere else in the chromosome group, individuals homozygous for the deletion might survive and give rise to another species. Then, if crosses were to occur between this "deleted" species and the "complete" species from which it sprang, pairing of chromosomes in the hybrid would bring together a "deleted" chromosome and a "complete" chromosome. Lack of matching genes in the region of the deletion could help to cause irregularities in meiosis which would result in partial or complete sterility of the hybrid.

Translocations, or the attachment of pieces of chromosomes to other nonhomologous chromosomes, have the same possibilities as trouble makers as do inversions and deletions. New species may perhaps arise if two such translocated combinations can be brought together so that the chromosomes of the new type can be paired. If two species differing in such a translocation were crossed the hybrid would face the same problem of pairing between chromosomes whose genes did not correspond throughout, and irregularities of meiosis could again cause sterility.

A special situation is created when translocation is an *exchange* between nonhomologous chromosomes; that is, when a piece of chromosome *A* is attached to chromosome *B*, and a piece of *B* becomes attached to *A*. Such interchanges are known as reciprocal translocations (Fig. 31, page 93). The consequences are rather too complicated for full presentation here. In general, the translocated *A* piece tends to pair with the corresponding portion of the unaltered *A* chromosome, and the translocated *B* piece tends to pair with the corresponding part of the unaltered *B* chromosome. As a result a ring of four chromosomes is produced instead of two pairs. If two or more reciprocal translocations have occurred, rings of six or more chromosomes may take the place of three or more pairs. The general scheme of ring formation is shown in Fig. 57. A species having such rings of chromosomes can be maintained in perpetuity, almost, by so-called "balanced lethal" genes which destroy certain combinations of the germ cells and allow to survive only those combinations which will again necessitate the formation of

chromosome rings. Since in the organisms, such as the evening primrose, in which chromosome rings are best known genetically, this arrangement does not preclude crossing with other species, the reciprocal translocations which bring it about are not to be regarded as sure sources of isolation of species; yet it does maintain certain combinations preferentially, which has about the same effect.

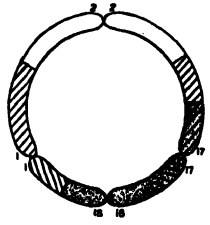


FIG. 57.—Ring formation instead of pairing, in chromosomes which have been reconstituted by reciprocal translocation. One chromosome is made up of parts of original chromosomes 2 and 1, another of parts of 1 and 18, a third of parts of 18 and 17, etc. Like parts tend to meet, forming a ring. (*From Sinnott and Dunn, Principles of Genetics, McGraw-Hill Book Company, Inc.*)

Intersexes and Interspecific Sterility.—Another quite different way of maintaining sharp distinctions between species through infertility of their hybrids is by the production of intersexes. These individuals possess a combination of male and female characteristics, or structures in some degree intermediate between those of typical males and females. Sex is very commonly dependent on a difference in the chromosomes, as indicated in an earlier chapter. In a very large number of animals, including man and the other mammals, many insects and some fishes, the female has two chromosomes of a particular sort designated the X chromosomes, while the male has only one X. All eggs have one X, while the spermatozoa are of two kinds, half of them containing an X chromosome, the other half lacking it. Eggs fertilized by the X-bearing type of spermatozoon develop into females, those fertilized by spermatozoa lacking the X become males. Thus the XX and X conditions are perpetuated in all generations. In birds, butterflies and moths and some fishes, a similar situation exists, except that it is the male which has two chromosomes of the special kind associated with sex, while the female has only one. In recognition of this difference, American biologists designate these special chromosomes Z. A male bird or moth thus has the composition ZZ, the female Z.

There appear to be a number of genes in these chromosomes, at least in some organisms, which determine sex, although their loci have not yet been ascertained. However, sex is not a simple character, and the X and Z chromosomes are not alone in determining it. From triploid ($3n$) individuals in Drosophila,

that is, flies that have three chromosomes of each kind instead of the normal two, it has been possible to obtain flies which are $3n$ for the X chromosome and only $2n$ or even only n for the other chromosomes (which are called the autosomes). Also, some flies are produced which are only $2n$ for the X chromosomes and either $3n$ or $2n$, or even only n, for the autosomes. Or the

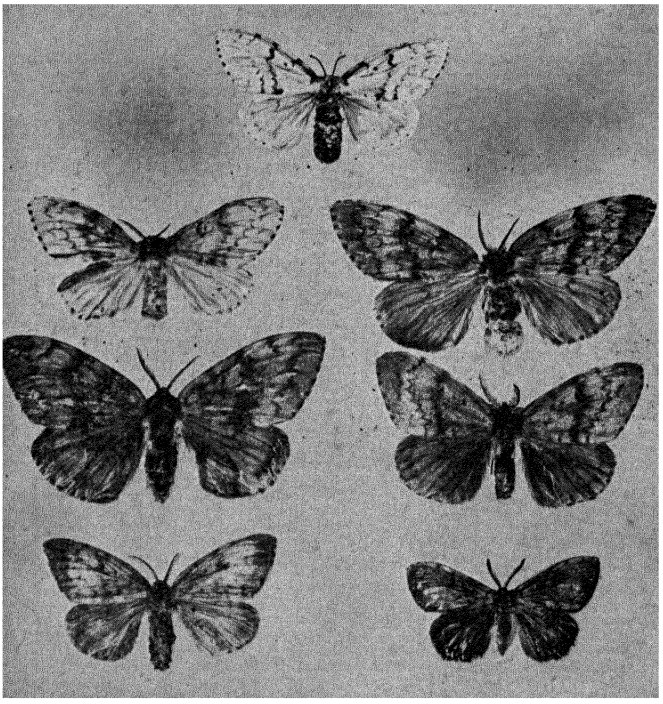


FIG. 58.—Intersexes of gypsy moth. Normal female above, various grades of intersexes below, and sex-reversed male at lower right. (*From Goldschmidt.*)

flies may have only one X chromosome and be $3n$ or $2n$ or n for the autosomes. Now, some of these combinations turn out to be intersexes of various grades. From them it is concluded that sex is dependent on a balance between the X chromosomes and some of the autosomes. A certain high ratio (1:1) of X chromosomes to autosomes makes a typical female, and a low ratio (1:2) of X chromosomes to autosomes makes a male; but ratios between these extremes produce intersexes.

This concept of sex as the result of a balance between chromosomes or sets of genes enables one to understand why in some instances the hybrids between species are intersexes. The best understood intersexes are not species hybrids, they are hybrids between races within the same species, but their production throws light on what is to be expected as between species. Goldschmidt has made extensive studies of intersexes in the gypsy moth (Fig. 58), in which intersexes regularly result from crossing certain races. He interprets his results to mean that

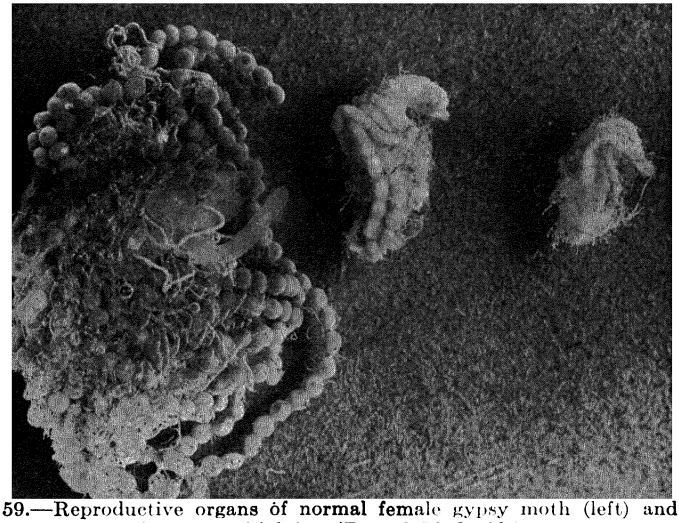


FIG. 59.—Reproductive organs of normal female gypsy moth (left) and two intersexes (right). (*From Goldschmidt.*)

there are "strong" and "weak" races in this moth. Any mating within a strong race, or between two strong races, yields the usual ratio to be expected from two Z chromosomes, or from one Z, and typical males come from the former, typical females from the latter. In like manner, matings within a weak race or between two weak races result in the balance that is normally to be expected from ZZ or from Z. When, however, a strong race is crossed with a weak one, ZZ in the hybrid may not establish the correct balance for a male, or Z the right balance for a female. Under these circumstances intersexes are produced.

The significance of intersexes for our present problem is that they are usually sterile. An intersex that deviates only slightly

from the type which its X or its Z chromosomes would make it is likely to have only its reproductive ducts abnormal. One which deviates greatly from the normal may have its ovaries (Fig. 59) or testes deranged. In either case it is likely to be incapable of reproduction. How important this type of sterility may be in preventing intergradation between species is obvious. A number of species hybrids which are sterile are recognized as intersexes, and it is probable that many sterile hybrids which seem to be typical males or females are really intersexual in some way.

Sterility Genes.—Still another means of producing sterility of hybrids is through the combined action of certain genes which, in our ignorance of their exact physiological or developmental effects, we may call genes for sterility. The kind of action required is adumbrated in tobacco, where East has found instances of both self-sterility and cross-sterility in different races. To explain one set of sterility phenomena it was only necessary to assume that there were three alleles, designated S_1, S_2 and S_3, of which one plant might have any two unlike genes. Plants would thus be S_1S_2, or S_1S_3, or S_2S_3. Now, the physiological limitations are such that pollen will not grow successfully through the style of a plant unless its gene of this set of triple alleles is different from both of the homologous genes which that plant contains. Thus, plant S_1S_2 could be pollinated only by S_3-bearing pollen, and such pollen could come only from an S_1S_3 or an S_2S_3 plant. Plant S_2S_3 could be pollinated only by S_1 pollen, which might come from either S_1S_2 or S_1S_3 plants. In this example the plants are self-sterile.

To account for cross-sterility we need only postulate a modification of the action of such sterility genes. We may suppose that sterility arises from a combination of certain complementary dominant genes which we may likewise call S_1 and S_2. S_1 alone produces no untoward effect, even when an organism is homozygous for it (S_1S_1). Likewise, S_2 is harmless, even in the homozygous state (S_2S_2). When, however, both S_1 and S_2 occur together in the same individual, they may be supposed to result in abnormal development of the reproductive system, or abnormal meiosis of the germ cells, or in some other defect which prevents or reduces reproduction. Under these conditions, if a given species is homozygous for S_1, and another species—otherwise quite capable of crossing with the first—is homozygous for

S_2, all hybrids between these species will be S_1S_2, and consequently sterile. Since this explanation is simply a way of accounting for sterile hybrids, it may be applied to any case of such sterility for which the reason is not clearly something else. Schultz and Dobzhansky are of the opinion that the hybrid between *Drosophila melanogaster* and *D. simulans*, referred to earlier, owes its sterility to such dominant complementary genes.

Geographic Isolation in the Light of Sterility Mechanisms.—In view of these means of effecting sterility, how is geographic separation to be appraised? The early supporters of isolation as a factor in evolution generally regarded this segregation of groups as an opportunity to accumulate differences. Sometimes the separated areas were considered to have somewhat different environmental features, and either to induce different modifications of the organisms in Lamarckian fashion, or to preserve different characters through selection. But even if they had recognized the apparently spontaneous occurrence of mutations and the accidental placement of the mutant individuals in the range of a species, or the random recombinations of genes in different populations, they could still have supposed that as a consequence of these changes two populations in different areas would gradually come to possess different sets of characters. The leveling effect of hybridization would be missing as between the groups.

Would these differences tend to make the two groups intersterile? It seemed to be assumed that they would. The existence of different characters in two animals was thought somehow to render them mutually incompatible. Discussions of isolation were usually generalized, and the details believed to make organisms incompatible were not specified. Sometimes differences in copulatory organs or other reproductive structures, or in physiological properties serving as sexual excitants were named as obvious cases in point, but the tacit assumption was still made that differences in general would cause intersterility. For otherwise, unless reproductive characters mutate much oftener than other qualities do, isolation should provide us many more species than there are that differ in visible respects but are not intersterile. The very great preponderance of sterility between species seemed to require that differences of nearly all kinds would, if great enough, lead to incompatibility.

It is doubtful whether this part of early isolation theory has much validity. When two species of mice differ principally in the color of the fur, the length of the tail and the shape of the ears, it is difficult to imagine that these inequalities prevent either mating, or the union of egg and sperm, or the production of viable germ cells by the hybrid between them. In genetics laboratories individual vinegar flies may be produced which differ in a dozen characters, any two or three of which would make them different species if only they could not interbreed, and yet they mate freely and produce fertile offspring. There is little in the ordinary facts of genetics to support the view that accumulation of differences of the kinds by which species are recognized and distinguished from one another leads to intersterility. If taxonomists were to change their technique and begin to describe species in terms of odors, senses and other psychological properties, chromosome composition and genes having physiological effects, the situation would be materially changed; but with present methods of classification there is little conceivable connection between specific distinctions and sterility.

Any genuine effect of geographic separation in producing species must therefore relate chiefly to other characters than the one by which species are discriminated. The thing that must owe its origin to isolation, if the latter is an important agent, is the sterility of one species with another. No one cause of intersterility can reasonably be expected to operate in all instances. Whether geographic isolation is a cause would seem to depend on whether the intersterility arises by a series of steps. Different odors, different times of breeding may originate as a result of geographic separation if they arise by a series of mutations, that is, if they are dependent on a number of genes. It is not known regarding most such qualities whether they are single-gene or multiple-gene effects. Any character arising by a single mutation could not accumulate because of geographic isolation, because it is full-fledged at the outset. Right- and left-handed coiling in certain snails are known to differ by just one pair of genes, hence this obstacle to mating can hardly have been dependent on physical segregation of any group. Yet there may be composite conditions, those that depend on many genes, and these could arise gradually and be accumulated with some aid from geographic separation.

Doubling of the number of chromosomes, on the contrary, presumably happens all at once by an abortive cell division in which the chromosomes are duplicated while the cell body is not divided. The union of nonhomologous chromosomes with one another is also but one short process. The addition of a single chromosome to the group through nondisjunction is likewise a single step. While the addition of several chromosomes of different kinds could occur in several steps, it also could, and probably does, occur at one time. Inversions, translocations and other chromosome aberrations occur suddenly, not gradually.

The features of X or Z chromosomes, or of other chromosomes, which distinguish "strong" and "weak" races, and so lead to intersexual hybrids, as indicated by knowledge of their genetics, arise by single mutations, and are not accumulations of numerous steps. And finally, the dominant complementary genes which may explain any hybrid sterility presumably originate suddenly, the potential hybrid sterility coming into existence at the moment when the second of these genes is produced.

How these single-step causes of intersterility could arise any better in separated groups than in freely interbreeding populations is not clear. Since, so far as known, most of these changes do not confer any disadvantage on individuals as individuals, appeal to any environmental differences in separated regions to preserve them is without point. The accidents of survival should enable one of these alterations to become established quite as readily in the midst of a general population as in a group on an island cut off from the main body of the species. Any surviving modification of one of these sorts could result in a group of individuals capable of breeding with one another but not with the rest of the population, even though this group mingled freely every hour of the day with individuals of the unaltered type.

Under these circumstances the change producing at least partial intersterility may well be at least occasionally the first step in the formation of a new species. A gene may arise which makes its possessor incapable of interbreeding freely with some portion of its species. The mutation may occur in an individual that is otherwise exactly like those with which it can not readily hybridize. It may occur at any point in the range, even in the most populous portion. An isolated group may thus be created

in the midst of large numbers of individuals not belonging to it. After this isolation, the accidents of mutation and of survival of individuals, plus the effects of any advantages or disadvantages conferred by mutations, may serve to develop a recognizably different species. Migration is of no concern, since hybridization with its leveling (not swamping) effect is precluded or greatly reduced. The order of events may well be, in a proportion of instances, intersterility first, visible differentiation next. The living world may have a quota of incipient species looking exactly like those from which they are springing. Whether they survive, differentiate, and gain recognition by taxonomists, is another and very different question.

To whatever extent intersterility arises in the sudden manner here described geographic separation loses in significance. Probably isolation of the geographic sort has been much overworked in evolution theory; but there are abundant other types of isolation to take its place.

CHAPTER XV

NONADAPTIVE CHARACTERS

> . . . numberless characters are produced in living things which are not useful at all. . . . THEODOR EIMER, 1895.
>
> . . . the developmental scene is filled chiefly with a rich byplay of all manner of nonutilitarian divergences. . . .
>
> A. GULICK, 1932.

The history of evolution theory has been dominated largely by the desire to explain adaptation. From the dawn of biological thinking the fitness of animals to their surroundings has appeared to most naturalists to be one of the marvels of the ages. Ancient stories dealt with the wonderful suitability of structures and instincts to the uses to which they were put, and often nothing short of divine wisdom and ingenuity, concentrated upon the animals' problems, seemed adequate to account for them. Even now, probably the majority of biologists, particularly those whose chief interest lies in what is called natural history, regard adaptation as the chief distinction of life and as the thing which above all else demands an explanation.

This awe and fascination of the useful have colored evolution doctrine from the beginning. The Lamarckian principle of the inheritance of the effects of use and disuse owed its plausibility to the fact that it offered an explanation of adaptive evolution in what otherwise should have been a chaotic world. The rapid acceptance of Darwin's natural selection was in part a consequence of its obvious relation to usefulness. The many modifications of the natural selection doctrine, such as the theories of sexual selection, warning color, mimicry, signal colors and the like were all results of the overpowering conviction that everything in living nature is in some way advantageous to its possessors. Moreover, it is a strain on human self-satisfaction to be asked to admit that mankind would be better off without some of his characteristics.

The Existence of Useless Characters.—To one who is not steeped, however, in the principle that whatever is is valuable,

and who is content to apply to utility the same standards of judgment as are applied to other qualities, it seems obvious that animals and plants are often possessed of features which are quite unable to perform any service for them. Attention was called in the first chapter to the fact that the differences between species of the same genus very seldom serve any function in the lives of the individuals which gives one species any advantage over the others. Even the differences between the genera of the same family are only occasionally of obvious function. The distinctions between groups of higher rank, on the contrary, are apt to be of some service.

Outside the field of taxonomy are many instances of apparent uselessness. Since the idea that qualities may lack a function is already an old one, it is only necessary to turn to the literature for examples. The paleontologists have often alluded to the great development of the Mesozoic reptiles and the Pleistocene mammals as instances of overspecialization. The implication in this term is that the curious spines, horns and snouts of some of these beasts were not only without advantage to them but were actually harmful. Some have regarded these excessive developments as the cause of the downfall of these great groups. We may waive for the present discussion the claim that these structures were harmful; if only they were useless—which many of them still appear to have been—they call for an explanation not provided by the adaptational theories of evolution.

Numerous characters in modern animals have likewise been listed among those without function. Eimer in his "Organic Evolution," as a prelude to a theory, soon to be mentioned, which was designed to account for nonadaptive characters, expressed himself as follows: "To what end the exquisite shapes of the Radiolaria, the exquisite sculpture, markings and colors of the mollusk's shell, which latter are, moreover, generally covered throughout life by mud and dirt, and whose beauty of line and color often only appears after polishing? To what end the black peritoneum of many vertebrates? To what end the delicately wrought patterns of the leaves of our foliage trees? To what end the whitening of the hair and all the other changes of old age in animals and in man? . . . Surely not for the advantage of the individual, nor that of the species." Cunningham, his translator, adds in his preface: "What is the use of the coiling of the shell

and the torsion of the organs in the greater number of gasteropod snails? . . . What is the use of phosphorescence to pelagic animals?" and then goes on to ask what adaptation to environment has caused starfishes to have 5 or 11 or 13 arms. Kellogg, in his "Darwinism Today" (1907), finds it extremely difficult to believe that the horny callosities on a horse's feet have any use. He also points to the triviality of the number of spots on the wing covers of ladybird beetles, the curve of a wing vein, the length of a hair, the number of rays in a fish's fins, and others.

These examples of what older naturalists thought were useless characters will enable any one at all familiar with animals to name many others which belong in the same category. Some one may say that we do not know the uses to which all characters are put, and that is quite true. Charles Darwin, and after him Romanes, devoted considerable space to debating the value of trivial qualities, Darwin in particular holding that very small differences might conceivably spell the difference between success and failure. Some of the qualities which have been called useless have, in the advancement of biological knowledge, been shown to have a use. An optimist, or one who desired at all costs to maintain natural selection as the sole guide of evolution, might look forward to a time when so many apparently insignificant features of organisms had been found to be of value that all the rest might reasonably be expected to join them in time. At present, however, that position can be taken only by the two classes named—the optimists and those who close their eyes. Literally thousands of characters exist for which no use can reasonably be imagined. Under these circumstances no general theory of guidance of evolution can be regarded as satisfactory which does not admit of change in useless directions.

Old Ideas of Internal Guidance.—This necessity of something to bring about nonadaptive change has been felt by some biologists in every generation since evolution itself came to be generally accepted. Some were content to point out that natural selection is incompetent to cover such cases, without suggesting precise substitutes. Some appealed to the direct action of the environment. The latter is not Lamarckian (though it is often called by that name), for Lamarck postulated change only through the effects of use and disuse, and change resulting from function would perhaps be supposed to be adaptive. Direct

modification of organisms by environment, not through use, would not necessarily be adaptive, and much support was given to this method of producing useless characters. Still others postulated internal agencies of unknown nature. Nägeli supposed animals and plants to be possessed of or governed by a principle of perfection which led step by step to greater complexity. No one has ever understood what sort of thing this perfecting principle might be. Nägeli himself appears not to have tried to understand it; it was a mystical concept which was supposed to require only a name. Von Kölliker also postulated "inner causes" amounting to a "general law of evolution." Embryonic development was supposed to respond to these inner causes and produce a new type of organism. At first there was no hint as to the supposed nature of the inner causes, but in von Kölliker's later writings it was made clear that they were held to be physicochemical. Even Weismann, who ultimately became the most ardent and most active champion of natural selection as practically the sole guide of evolution, in his earlier writings presented evidence that some of the direction of evolution comes from within the animals themselves. While he was unwilling to postulate an unknown transmutation force, or special evolution principle, he was driven by the parallel evolution of different species to suppose that there is an internal law of evolution which determines the future modification of species. Cope also emphasized that evolution took place along certain lines, though it is not clear that the internal constitution of organisms or any other internal agency was held by him to do the directing.

Orthogenesis.—The most extensive development of the idea that the direction of evolution is determined from within is that brought out by Theodor Eimer. For his "definitely directed evolution" Haacke invented the term "orthogenesis," which Eimer subsequently adopted. The word literally means development or evolution in a straight line. From its derivation the name might be applied to any change consisting of successive steps of the same sort regardless of their cause. There is some confusion, however, in the use of the term, related chiefly to whether it applies to change directed by external agencies or not. Guidance might conceivably come from (1) direct modification of animals by the environment, (2) preservation only of certain lines of modification, and (3) some directing force within the

organisms. The first two are external, the last internal. The first may be dismissed as involving either inheritance of acquired characters, against which modern genetics speaks very strongly, or the determination of the direction of mutation by the environment, which plainly does not occur in the mutations whose causative agents have been discovered. The confusion in usage relates to the second and third possibilities, one involving natural selection, the other an unknown internal agency. Are changes due to both these causes, assuming that they exist, properly called orthogenesis? The fundamental distinction between them was recognized by some biologists, and by them the term orthoselection was proposed for straight-line evolution guided by selection, thus leaving the word orthogenesis for straight-line evolution directed by an internal factor.

The latter meaning was the one attached to orthogenesis by its chief sponsor Eimer. He constantly bolsters his theory by calling attention to the nonadaptive nature of many characters of organisms. He could not consistently rest his case for orthogenesis on such characters if he supposed the straight-line evolution to arise out of selection, for selection should make the characters useful. It has often been said that Eimer supposed orthogenesis to be an environmental effect. This impression is due no doubt to confusion of the *production* of change with the *guidance* of change. Eimer did assume that evolution (meaning modification) is *stimulated* by external conditions, but expressly and repeatedly maintained that the *guidance* of the change is due to something within the organisms. Orthogenesis is a result of this internal guidance.

Eimer conceived evolution of races to be something like the growth and embryonic development of individuals. An individual follows a set course of development, it grows in accordance with certain physiological rules. So, he thought, populations grow and develop in harmony with established rules of growth. Change, evolution of the population would occur in a foreordained way, producing species and higher taxonomic ranks as part of the operations of the laws of growth, just as changes of juvenile and old-age characters take place in individuals in predictable fashion. In Eimer's day little was known of the rules of individual development. Today we understand some features of it, in terms of physiological gradients, relative posi-

tions of parts, and successions of hormone effects. Does this knowledge help us any in understanding the differentiation of races? Probably not, for in individuals the course of development is dependent on actual contact of tissues with one another or on some avenue of communication between them. When one looks for the contact between parts of a population, it can not be found in higher organisms (those not colonial); and as for an avenue of communication between individuals in a population, the germ cells in lines of descent furnish the only possible one. Hence, if there is any law of growth which guides evolution, it must operate through the germ cells. The problem of orthogenesis in Eimer's sense thus devolves upon the geneticists.

Orthogenesis Not Synonymous with Nonadaptive Evolution.—Before proceeding to the suggestions which geneticists have made as to the mechanism of orthogenesis, it is well to be perfectly clear that orthogenesis is not necessarily nonadaptive and that it does not comprise all of nonadaptive evolution. While orthogenesis in Eimer's sense would most of it result in useless characters, it could on rare occasions, purely as a matter of chance, lead to adaptive modification. Also, evolution is not orthogenesis unless it proceeds along the same course for at least several successive steps. A single step, even if not useful, is not orthogenesis. Furthermore, if evolution were to lead to a certain end result by a tortuous path instead of a straight one, that would not be orthogenesis, even though it were useless throughout the process.

The reasons for considering orthogenesis so seriously in seeking the origin of nonadaptive characters are that most of it is certain to be nonadaptive, and that it has attracted so much attention as to have been studied. It is chiefly those long series of nonadaptive changes that have appealed to naturalists as constituting a problem. If orthogenesis could be satisfactorily explained we would doubtless have a solution of most, if not all, of the problems of the origin of useless characters. But in our search for the mechanism of nonadaptive change, we need not limit ourselves to the orthogenetic examples of it.

Possible Orthogenesis in Mutation.—We are already familiar with the fact that mutation is not random, but is directed in accordance with the structure of the genes. It is also clear that repeated mutation of a gene to one of its mutant forms

should eventually establish the mutation in the population in place of the original gene, provided the mutation is not in any way harmful. A nonadaptive character constituting a single modification could thus arise by recurrent mutation. If, now, there were any tendency for successive mutations of a gene to go farther and farther in the same direction, and if none of the mutant forms was harmful, and if the mutations occurred repeatedly, an orthogenetic change would take place.

There are so many "ifs" in the above supposition that no one had, until recently, imagined that any genuine evolution might have occurred in this way. Jollos, however, on the basis of some experiments with Drosophila which have already been mentioned (page 131), suggests that orthogenesis could actually result from successively more accentuated mutations of a certain type. Following the lead of Goldschmidt, Jollos caused mutations in the germ cells of Drosophila by applying heat to them in the young stages of the flies. He reports that in some of the characters affected, notably the color of the body, he found a tendency for successive mutations in the same line of descent to be more and more marked. The color of the body, for example, became darker and darker as a result of these successive changes.

The experiments have been repeated by Plough and Ives, who confirm the production of mutations by heat, and some of the other special features of the original work, but do not find successive mutations going farther and farther in the same direction. The work of Jollos stands alone, therefore, in this particular development. Until it can be verified by others no emphasis can be put upon it as a way to an understanding of nonadaptive evolution.

Chance and the Production of Useless Characters.—In an earlier chapter chance was discussed as one of the factors of evolution. Obviously to whatever extent the agencies of evolution are purely random they are more likely to produce useless results than beneficial ones; for there are many more ways of being neutral than there are of being beneficial. There are many more things that can be done to a watch that leave it unhelped and unharmed than there are that improve it. The events that result in real deterioration are likewise presumably more numerous than the ameliorating ones, but they may be

left out of our present discussion since natural selection operates to remove them and does this so effectively that the worst ones are never even detected.

The accidents involved in the production of useless traits are simply those that operate in any evolution through the Mendelian mechanism. It is to some degree a random matter what genes mutate, though not altogether so. There is chance in the collection of genes in the germ cells, chance in the union of germ cells of different content in fertilization, chance in the survival of individuals of different sorts, chance in the pairing of different kinds of individuals in reproduction, and chance in the alteration of the population by migration. As a result of all these accidents, useless mutations may arise, or useless characters spring out of certain gene combinations; individuals possessing useless qualities may increase in relative numbers even to complete ascendancy; and populations in different areas may come to be different with respect to useless characters.

So long as only single neutral changes are in question, chance may be relied on to establish a certain percentage of them. When, to produce a given result, it is necessary that one particular event occurring at random must be followed by a specific other event which is accidental, and this in turn by a third that is dependent on chance, the likelihood is greatly reduced. And yet one may occasionally witness the throwing of dice—honest dice—which turn up double-six three or four times in a row; or sit through an evening of bridge and never receive more than one face card in the deal. Among the billions of changes that enter into evolution the unexpected must sometimes be expected.

Wright, as has already been pointed out, has calculated some of the possibilities of chance in evolution, and concludes that the differences between varieties of one species, or even between species of the same genus may be due to chance. If this conclusion is correct, one of the difficulties that have beset the natural selectionists ever since the beginning of their doctrine's history has been removed. The testimony of nearly all taxonomists that "specific characters" (the differences between allied species) are not adaptive is no longer a stumbling block to selection theory; the nonadaptiveness simply has another explanation.

Chance as the originator of uselessness cannot, however, be assumed to operate much beyond the small distinctions just discussed. It cannot be used to explain the generally assumed overspecialization of the dinosaurs or the titanotheres. The probability of a fortunate outcome decreases rapidly with increase in the number of single chances involved. One may be consistently unfortunate in the deals of an evening of cards, but hardly through a lengthy tournament.

Correlation of Nonadaptive with Adaptive Characters.—One way of explaining orthogenesis or any other nonadaptive evolution is to suppose that the indifferent character is closely correlated with, or another expression of the genetic basis of, some useful character. If spines were but a morphological expression of the presence of some fertility factor or some disease-resistant substance, and if spines grew larger as the beneficial substance became more effective, there would be a plain basis for nonadaptive evolution of spines as a result of selection. Complete identity of the genetic basis of the useless character with the genetic basis of the beneficial one would not be necessary; if an important fraction of the genetic basis were common to both, nonadaptive change would result from selection but in lesser degree. Correlation used to be assumed as if it were a separate factor, just as orthogenesis was assumed as a principle by itself; but what is needed is a physiological mechanism to explain it. Linkage of the genes for two characters in the same chromosome, as we have already seen, will not do, since breakage of the linkage is followed by a line of descendants in which the two characters are kept apart as much as they were previously kept together. The net result of linkage in a long-time process like evolution is, as a factor in correlation, precisely zero. No satisfactory means of correlation of neutral characters with useful ones, other than a fractional or complete identity of their genetic bases, has yet been proposed.

Something like correlation—at least a linking of a useless with a useful thing—has been suggested by Haldane. He conceives that a useless feature of an adult organism may be in some way beneficial in the embryo, and might even be carried to greater and greater development because of its selective advantage in the young stages. Haldane mentions no example, and probably has none in mind. Certain mutations in Drosophila do include

larval differences that have no observable relation to the adult modification; but while the latter seem to be useless, there is no indication that the former are beneficial. Surgeons have commonly refrained from removing the tonsils of very small children on the ground that they might have a developmental function, but the latter has never been demonstrated.

Possible Consequences of Size.—What may be regarded as a form of correlation of the sort just discussed is the connection which probably exists between size and structural modifications. The idea goes back at least to the work of Klatt on the skulls of



FIG. 60.—Successive antlers of the wapiti or American elk.

dogs in which it was shown that the skulls are of different proportions in individuals of different size. Also, it is matter of common observation that body proportions change with age. A child does not merely increase in size as it grows, but it changes in shape. It grows faster in some directions and in some parts than in others. This change in proportions may sometimes appear to be the production of a new character. Or the same principle may actually lead to a new character. It is well known that members of the deer family, whose antlers are shed annually, develop successively more branched and larger antlers year after year (Fig. 60), up to a maximum which may be regarded as the individual's peak of development, and after that time there is a decline in the size of the antler. This change corresponds roughly to the evolution of antlers, except perhaps the decline late in life, and these structures have often been used as an example of the operation of the biogenetic law. Also, the

deer tribe have grown larger as part of their evolution, just as they grow larger in individual development.

Here is an age effect that is particularly significant because it is not necessarily modified by what has been produced at an earlier age. The antlers completely disappear, and are regenerated in accordance with the physiological conditions then obtaining, without the necessity of modifying antlers already in the way. Hence the renewed structures should give an accurate representation of the animal's physiology as it exists in the season of renewal. J. S. Huxley has made the suggestion that the antlers are successively larger and more branched because the animal as a whole is larger. The genes present one year are identical with those of the preceding year (unless there be progressive mutation of the genes in the body cells such as Wright suggests occurs in the production of color pattern, as described on page 193). In other words this is one of the very common situations in which the very same genes do different things depending on the conditions in which they are immersed. Huxley thinks of the surrounding conditions as merely those of size. The genes of a deer in a small animal produce a small and simple antler, the same genes in a larger animal produce a larger and more branched antler. Perhaps the condition is not merely one of size; it may rather be a physiological condition *one* of whose consequences is size. This seems the more likely since the antlers decline in size in older animals without any known decrease of body size in old age. The distinction is not, however, a very important one if the physiological condition in question is, as it seems to be, rather closely correlated with size. Increase of size, or progressive change in the agency which determines size, carries with it a change in the size and shape of the antlers.

Now, as explained earlier, the evolution of the deer family has involved an increase in body size, and an increase in size and complexity of the antlers. The suggestion is near at hand, and Huxley makes it, that the evolution of the antlers has been a consequence of the evolution of size. There need have been no change in genes or groups of genes specifically responsible for antlers; there need only have been a change in the genes for size—which turn out to be also in this instance genes for antlers. It is immaterial whether we think of this as evolution of the antlers at all; it is one of the series of progressive changes which

has been called orthogenesis, whose adaptiveness has been debated, and it calls for explanation.

If antler size and complexity are but expressions of body size, increased antlers need not be adaptive in order to be controlled by natural selection, if only increased body size is useful. If larger size is beneficial, and natural selection is able to bring about such increase, then the size and branching of the antlers should follow as a by-product. Is larger size useful? It is plain that in some of the ordinary activities of living things large size *is* useful. The larger members of a litter of pigs or other mammals, as Castle has pointed out, can shove their smaller brothers and sisters away from the banquet table. Whether size is valuable in the evolutionary sense—that is, whether it leads to more descendants—is not so certain, but there is no evidence that it is not useful. Paleontology furnishes many facts which receive a simple explanation if large size is beneficial, for in many groups increase of body size is one of the prominent features of their evolution. The classical lines of evolution of the horse, camel and elephant all involve such increase. The mammals in general furnish many examples of growth in size up to Pleistocene time, after which there was a general destruction of these great beasts. The huge reptiles of Mesozoic time form in general a progression in size up to the time of their disappearance in or after the Cretaceous. The suggestion that large size is advantageous has, then, some circumstantial support as well as some promise as an explanation of certain of the difficulties of the natural selection theory.

Antlers of deer probably do not stand alone as by-products of size. The great titanotheres (mammals) had curious nasal prominences, and the dinosaurs had many horns, plates, fins and shields. Even if some of these may have been useful in attack or defense, they may well have owed their existence to the value of size rather than to their own use. They are not as good examples of correlation with size as antlers are, because we have no modern animals of these types, and the curious structures were not shed annually, so that we have no knowledge of their changes with the growth of the individual. Nor is size the only feature of organisms with which useless structures could be correlated. It is quite possible that spines, brilliant colors and color patterns of insects are but incidental consequences of other

things which may or may not be useful, and efforts to find their own value are futile.

Restrictions upon Variability.—One other possible source of orthogenesis should be mentioned because it may have a genetic explanation. That is an assumed tendency of the possible paths of evolution to become less numerous as specialization proceeds. There is an old view that as an evolutionary line advances the variability of its species decreases. That is, after certain paths have been chosen, so to speak, at the forks or crossroads, fewer divergent ways are thereafter presented. If such restriction occurs, and is carried far enough, only a single road may eventually be left open. What is meant may be illustrated—but not explained—by supposing the evolutionary possibilities of a group to be represented by a forest of conical trees, set just close enough for their lower branches to meet and intertwine, but whose upper branches are wholly apart from those of other trees. Let species be represented by caterpillars or other leaf-eating insects, and their variability be represented by their opportunity for *horizontal* spread. Suppose the caterpillars to start on the leaves of the lower branches, and let their evolution be represented by their upward progress as they devour the leaves of the trees. At the start, their variability—their capacity for migration laterally—is as wide as the forest. As they get higher they lose contact with neighboring trees, earlier on some sides than on others. Eventually the leafy part of each tree is separate from all others, and the horizontal migrations of the caterpillars are limited to the width of the tree. This width decreases as the leaves are devoured upward, until only the one terminal twig is left. Progress of the caterpillars is then limited to this one path.

Is there such gradual diminution of the open paths of change? Many evolutionists have believed in it, though it is quite likely that they have been led to this belief by their desire to explain observed instances of orthogenesis. There is also a widespread belief that evolution is irreversible; that is, that a line of descent, having taken a certain evolutionary course, is unable to retrace it. Again it is probable that the reason for making this assumption is the fact that whatever evidence there is of the course which evolution has taken reveals no instance of such reversal. We see what has or has not happened, and then enunciate a law

that it does or can not happen. So far as the primary steps of evolution—the mutations—are concerned, evolution may be reversed, for mutant genes have sometimes reverted to wild type. It is nevertheless possible that the occurrence of certain changes renders certain other modifications less likely. It may be that the probable kinds of future change are thereby made not only different but less numerous. It is not easy to picture this result on the basis of anything now known of genetics. But if we knew more of the structure of genes, and of the physicochemical nature of their interactions, it might be possible to discern why, after certain changes had taken place, the number of paths of further change open to them would be less.

Some of the best modern geneticists have plainly held that such progressive restriction of the paths of progress may actually occur, though none of them has ventured an explicit statement of its supposed mechanism. Wright, who has contributed as much as any one to the modern concept of evolution, and who assumes that minor degrees of nonadaptiveness are due to chance, as explained earlier, regards such restrictions as a possibility. Referring to the long-continued orthogenetic changes, like those of the Mesozoic reptiles, and to the belief of some older evolutionists that these changes gained a momentum that carried the species too far and were thus the cause of their destruction, he writes as follows: "Nonadaptive orthogenesis of a positive sort, increase of size of organs to a point which threatens the species, constitute a more difficult problem, if a real phenomenon. Probably many of the cases cited are cases in which the line of evolution represents the most favorable immediately open to a species doomed by competition with a form of radically different type or else cases in which selection based on individual advantage leads the species into a cul-de-sac." The paths *immediately open* apparently refer to a restricted degree of variability, while *cul-de-sac* presumably means still further restriction of the open paths to a group none of which is suitable to the given environment.

Goldschmidt frankly holds that genes control the whole process; that whether mutations occur, or what kind they are if they do occur, is determined by the gene complex as a whole. Such control, if it exists, would be as good a mechanism for guidance of nonadaptive evolution as any proponent of ortho-

genesis could wish. Goldschmidt has not, however, indicated the genetic particulars of the mechanism he proposes.

Blum would explain orthogenesis as a result of a thermodynamic principle that the earth's quota of free energy must steadily decrease. This principle leads him, however, to conclude that evolution is irreversible, which, as we have seen, is not true of mutations. It is not clear, moreover, why absence of return evolution should mean necessarily a straight advance in the direction previously pursued rather than a fan-shaped advance in all directions except the return. Any way, general evolution theory in terms of energy is not at the present time likely to prove very illuminating with respect to concrete changes.

Nonadaptiveness Still a Problem.—Notwithstanding the value of the suggestions already made, the explanation of useless characters can not yet be regarded as satisfactory. Here lie some of the most important of the outstanding problems of evolution. The progress made lends hope that solutions for them will eventually be found, but the advance promises to be slow. If a conjecture concerning the chief source of enlightenment is permissible, let it be said that it is probably to be found in a much wider knowledge of the forces involved in the development of the individual. Advances in this field will be watched with much interest and, it is to be hoped, shared in by students of evolution.

CHAPTER XVI

GEOGRAPHIC RACES

> It seems highly probable that the formation of these geographic races or subspecies represents one among the various modes in which the divergence of species and even larger categories of living beings has had its inception. F. B. SUMNER, 1929.
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> There is in my opinion no reliable fact known which would force us to assume that geographic variation or formation of subspecies has anything to do with species; the results of genetical analysis and of sober evaluation of the other facts are positively in contradiction to such an assumption. R. GOLDSCHMIDT, 1933.

While all genetic variation within a species is material with which evolution may build, any tendency for unlike types to occupy different areas is of especial interest in the problem of the origin of species. Not only are such groups the substance out of which modification by recombination may be derived, they give the appearance of having already taken on one of the characteristics of species. As indicated in the opening chapter, each species occupies an area which is different from that of nearly every other species. This area is regularly a continuous one, so that when rarely two groups of individuals visibly alike are separated by a wide gap they are regarded with suspicion as being perhaps not after all derived from a common stock. While species ranges overlap, the duplication of range is not usually important between those species which are most closely related—or, in nonevolutionary terms, those which are most alike. When, therefore, two groups existing within a species but having observably unlike characteristics occupy chiefly different areas, it is natural to ask whether these groups may not be on the way to divergence into distinct species. That question does not promptly arise in relation to differences exhibited by individuals within the same area. When we see brown and black bears of the same species roam the same woods and even spring from the same parents, or black and gray members of the so-called gray squirrel species caper through the same trees, we *may* be

witnessing the start of successful evolutionary divergence, but it is only a start. All that has happened so far in either of these instances is the occurrence of a mutation and its establishment in the population. When in addition to mutation and establishment there is territorial separation, the temptation to suspect the current formation of species is much stronger.

If such geographic races are incipient species, their characteristics and their mode of origin are of the utmost importance to evolution theory. Taxonomists and biogeographers have everywhere turned upon such varieties a scrutinizing gaze. Their interest centers in the questions how the varieties became different, how they came to occupy different areas, and whether species in general have regularly or often passed through a comparable phase. While it is seldom possible to obtain an answer to any of these questions from historical records of geographic races, a knowledge of their genetic composition and of the general method of evolution should enable one to draw inferences concerning them.

Genetic or Environmental?—A prime requirement of any relation of the varieties to evolution is that they rest upon hereditary differences. Before the advent of modern genetics there was little information on which to base an opinion, and views of the significance of geographically separated types were often radically opposed to one another. Some facts suggested on their face an environmental origin. When mammals had a northern and a southern form differing in color, it was possible to attribute the differences to the effects of temperature. In some old experiments in which pupae of butterflies were subjected to abnormally low temperatures there emerged from them insects having a pattern and colors resembling a more northerly variety of the same species, and there was room to suppose that the two varieties were genetically alike but responded differently to different temperatures in their development.

Some geographic variations, moreover, show a more or less steady change in keeping with an environmental gradient. Thus the gypsy moth, as Goldschmidt shows, varies with respect to the strength of its sex genes (to be discussed later) from northeast to southwest through Japan and Korea, and with respect to its color (light to dark) on the mainland from Korea to Manchuria. In like manner a species of the deer mouse Peromyscus, as

described by Sumner, becomes irregularly darker from the coast of Florida for a hundred miles into the interior in Alabama. So long as the genetics of such graduated variations was not known, it was possible to suppose they were of environmental origin. Many mammalogists appear to believe that geographic variation in color of the small mammals is in some way dependent on humidity, though this conclusion is based mostly on correlation of color with humidity of habitat, not upon any experimental test of the effect of moisture (see also page 258).

Breeding experiments by Sumner showed that some of the characteristics of his mice responded to such environmental factors as temperature, and he was inclined at first to conclude that geographic races were in large part of environmental origin. Later, however, when such races were brought into the laboratory and reared side by side, the differences observed in nature persisted, showing that they were plainly genetic. His results are conclusive for the races tested. Dice has demonstrated the inheritance of the color traits of some other races, particularly of the deer mouse. Goldschmidt, too, has done an enormous amount of genetic work on the gypsy moth, all of which goes to show that the differences between geographic races are inherited. This is true not only of the sex genes and color factors mentioned earlier, but of the length of time spent in the developmental stages, which is different for the different races, of their resistance to infectious diseases, of the size of the body, and of the number of times the caterpillars shed their skins.

Considering the smallness of the number of geographic races which have been adequately tested by experiment, and the near unanimity of these tests in indicating that their differences are at least in part hereditary, one is probably justified in concluding that such territorially separated varieties are as a rule genetically different. It is entirely pertinent, therefore, to pursue further the question of the relation of such races to the evolution of species.

Extent of Genetic Differences between Races.—An important part of the answer to the question how geographic races became different depends on how different they are. The work already done in this field indicates great variation in the amount. Goldschmidt concludes that the gypsy moth races differ from one another, with respect to the strength of their sex tendencies, in

just one gene. There are at least eight different male-determining genes, multiple alleles, that is, occupying the same locus of corresponding chromosomes of the various individuals, and of these any *stable* race may have just one. There are at least seven different female-determining genes, of which each race has just one. The color markings of the caterpillars are likewise, he concludes, due to genes at the same locus, so that each race has but one pair of them. Light color is dominant over dark in some races in young larvae, but recessive in older ones. There is, however, a cytoplasmic effect which makes the hybrids lean more to the maternal color. In the foregoing characters, while the large number of multiple alleles makes the genetics of the species as a whole rather complex, the contrast of any one race with any other race is fairly simple. Not so clear is inheritance of the duration of development, for the facts seem to call for one principal pair of genes and several modifying pairs.

In mice the genetic differences are less simple. Dice finds that even within a single geographic race of deer mice, *Peromyscus maniculatus blandus*, the two colors, gray and buff, are not just one pair of genes apart in their composition. While in general gray is recessive to buff, there are intermediates, and one must probably assume that there is one chief pair and several modifying pairs of genes. Sumner, after extensive breeding tests with mice, states that not one of the geographic races differs from any of the others by just one pair of genes. Nevertheless, segregation of characters after a more complex scheme is clearly indicated, and independence of the segregation of different characters is shown by correlation studies.

Differences other than ordinary genetic ones have been demonstrated in several instances. In the gypsy moth, while the reduced number of chromosomes is the same (31) in all the geographic races, the aggregate size of the chromosomes (mass of chromatin) is larger in the so-called "weak" sex races than in the "strong" ones. In timothy (*Phleum pratense*), Gregor and Sansome report a remarkable difference in chromosome number, 42 in one race and 14 in the other, within the same species. These two forms tend to live in different habitats, the former being the hay type, while the latter is found chiefly in natural pastures. Another species of the same genus (*Phleum alpinum*) likewise has two varieties, a 28-chromosome type in

Scotland, a 14-chromosome form in Sweden. Although timothy has long been cultivated, these examples of racial distinctions are probably not greatly vitiated by human interference, for the cytological studies were made on wild populations. In the locust Circotettix Helwig observes that bent and straight chromosomes of certain pairs are found in different proportions in different areas, and discusses the possible bearing of such chromosomes on the formation of geographic races; but at the present time no area is strictly and sharply characterized by any given combination of these chromosomes, and the locusts do not fall into recognizably different geographic races based on visible qualities.

The terms in which the differences between geographic varieties have been described are all such as are used in describing genetic phenomena in general. The behavior of the racial differences is, in nearly all cases where it is known, Mendelian in the broad sense of chromosomal. It is to be assumed, therefore, that they have arisen through changes in the Mendelian mechanism of some of the same general sorts as are assumed to have been responsible for evolution as a whole.

Mendelian Phenomena in Species Crosses.—These conclusions encourage a further examination of the possible relation of present geographic races to future species. If the differences between species are likewise Mendelian characters, most of the a priori objections to regarding varieties as embryonic species would be removed. We have already discussed the not uncommon crosses between species, and the varying degrees of fertility of their hybrids, as a source of recombination leading to further evolution. From some of the facts there related it could be inferred that the species characters are Mendelian, but this feature may now be specifically pointed out.

The most crossable species known are probably those of the genus Antirrhinum, the snapdragons. Among their hybrids there is high fertility and free recombination of the characters differentiating the species. But these are admittedly exceptional, and it seems better to rely chiefly on the behavior of specific characters in crosses which result in somewhat infertile hybrids. One feature of such hybrids is that in general all that come from a common source are pretty much alike. That is, species hybrids are about as uniform as are the F_1 generations

between varieties. This means that whatever is handed on by each parent to the species hybrid is assembled in some regulated fashion and is approximately the same for all, and that the characters of the hybrid are determined by this regulated contribution. Chromosomes are the only known mechanism which is so regulated. Then, too, the dominance relations of contrasted species characters to one another are of about the same order as are those of the more complicated varietal characters. In some instances, the character of one species is dominant over the corresponding one of the other species, and the hybrid may show dominant characters of both species. More often, however, the hybrid is in some degree intermediate, just as are some hybrids between varieties of the same species where the intermediacy is due to multiple genes. The two are not, therefore, very different as respects the mode of inheritance of their characters.

Even when fertility of the hybrids is very low, there is abundant reason to connect this fact with chromosomes. Rearrangements of genes by means of inversions or translocations may help to render meiosis abnormal in the hybrids, though there is less reason now than formerly to think that low fertility is commonly due to such misplacements. Even fertility itself is a character depending on chromosomal genes in some well understood cases, and dominant complementary genes are a satisfactory explanation of intersterility of types.

It is apparently possible, therefore, to account for all the differences between species on the same general basis as the differences between local races. The genetic differences between species may be the greater ones, but they are not of a wholly different order. Distinctions between species may involve a larger proportion of rearrangements within chromosomes, or exchanges between chromosomes, or alterations of chromosome number, than do varietal differences, but they are chromosomal in one way or another.

Adaptiveness of Geographic Races.—If local races and species are sufficiently alike in genetic composition that the former may be leading to the latter, it is important to discover how the races came by their spatial separation. Since selection is an obviously possible method, it is pertinent to inquire whether the separated varieties are in some way specially fitted to the areas

in which they are found. Goldschmidt finds a very important adaptation of the gypsy moth races to the regions which they inhabit. Largely it is a relation to temperature. The several races have different speeds of development, which cause them to emerge at different times in the spring. Since the larvae dare not appear before vegetation is available as food, and since they must not continue later in summer than food is still available, it is obvious that different races will best fit different areas. Single mutations have changed the speed of development in certain individuals, and have thereby immediately fitted them for other regions where the winter is either shorter or longer. With good luck some of these mutants reached such regions and their descendants became established there. Now, these changes in the speed of development also cause changes in the color, and the new area is peopled by a visibly distinguishable race. The whole process as Goldschmidt conceives it is one that was sponsored by Cuénot and Davenport and by the former called preadaptation. First a change occurred, fitting individuals for a new situation, and then sometimes the new situation was either near at hand or was accidentally reached.

The adaptiveness of some other geographic races is not so obvious. Among the mice it is common to find separated races that more or less resemble their general background, and the prevailing view has been that they are protectively colored. Three varieties of the deer mouse *Peromyscus polionotus* differ thus in relation to the soil of their respective regions. The variety *leucocephalus* occupies white sandy areas, *polionotus* is in regions of darker soil, and *albifrons* in regions of intermediate shade. When all three of them are put on dark soil (Fig. 61) it is obvious that *leucocephalus* is more conspicuous than the others, and when all are on white sand (Fig. 62) *polionotus* is the conspicuous one. If it may be supposed that the enemies of the mice overlook them when they merge with their surroundings, a neat explanation of their present geographic separation is provided. Sumner is apparently convinced that this is at least part of the explanation. Dice supports this view on the basis of comparisons made elsewhere, as does also Benson. Sumner and others have endeavored to discover other factors which might account for the color differences, but no other explanations seem applicable to the mice. Sumner has adopted the

protective coloration theory because of the inadequacy of other explanations, but has done so cautiously. Other investigators, however, consider this solution so plausible that they have not felt it necessary even to look for any other.

Not all geographic races appear to be adaptive, however. Crampton has made a very extensive study of the snails of

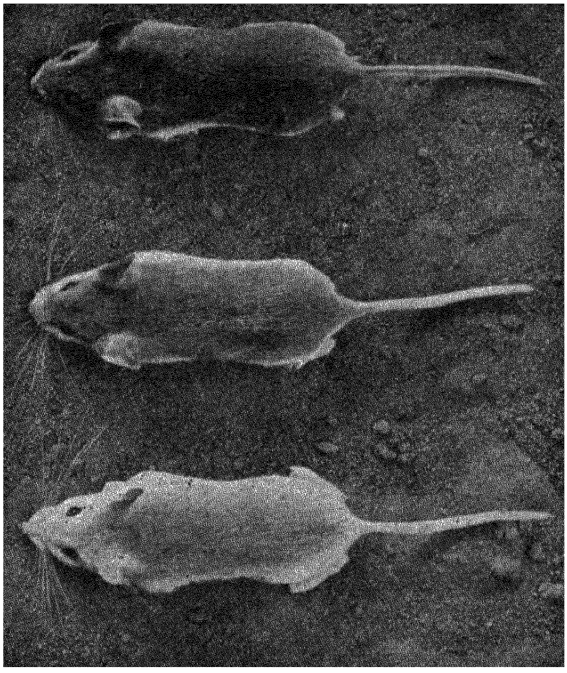


FIG. 61.—Three color varieties of *Peromyscus polionotus* on dark soil. Above, variety *polionotus;* middle, *albifrons;* below, *leucocephalus:* (*From Sumner in Bibliographia Genetica.*)

Moorea, one of the Society Islands. Division of the species into groups with more or less different characters and occupying different areas seems to be almost the rule among these animals. To take just one example, *Partula suturalis* is divided into two races, one occupying a group of contiguous valleys in the southeastern part of the island, the other being spread over much of the rest of the island. The two groups differ in color and size, the southeastern group being the smaller. The direction of coiling is also different in a statistical sense, for the south-

eastern group is exclusively dextral, while the northwestern group is sinistral in some subareas, dextral in others. The evidence from distribution goes to show that this northwestern mixed group started out dextral, became sinistral in certain portions of its area as it spread, and then finally returned in one part to the dextral form. Of these several colonies Crampton

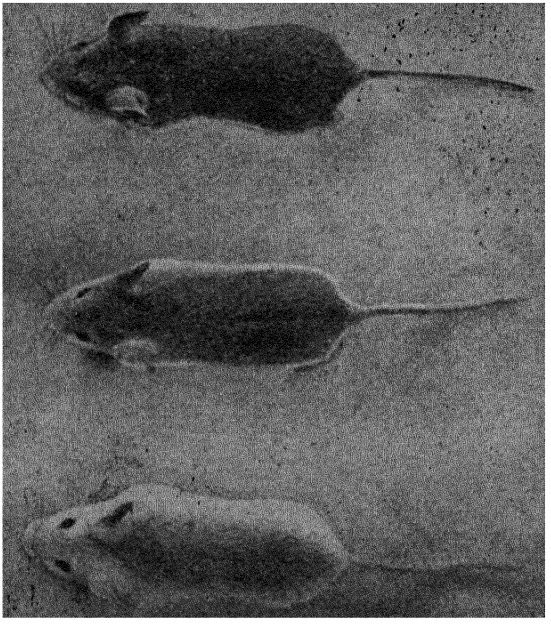


FIG. 62.—The same color varieties of *Peromyscus polionotus* as those in Fig. 61, but on white sand. (*From Sumner in Bibliographia Genetica.*)

says their structural differences are "without any relation to discoverable environmental circumstances."

The same is said to be true of the grosbeak family Geospizidae of the Galapagos Islands. It seems almost certain that all members of this family are descendants of one immigrant stock. They have become very diverse with respect to the form of the bill and other characters usually relied upon as means of classification, and the different forms tend to occupy different areas. Since the beak is used to obtain food, of kinds available in very dissimilar situations, it might be supposed that the various forms of the beak would be adjusted to corresponding sources of

food. However, while the genera of these birds do show such adaptation to particular stations, this is not true of the geographic races within any one species. Gulick is of the opinion that natural selection can not be operating upon them to any extent.

It seems clear from all these observations that, although usefulness in different situations may sometimes be the cause of the geographic separation of unlike forms, it can not be alone responsible for all such phenomena. Probably the accidents of place of mutation, accidents of survival and accidents of migration may account for some areal divergence.

Physiological Basis of Geographic Races.—The more fundamental reasons for the differences between geographic varieties are of importance, though not much is known concerning them. Speed of development has already been pointed out as the distinguishing character of the gypsy moth races, according to Goldschmidt. The details go far beyond the mere fitness for a winter of a given duration, which is the adaptive feature. There are light and dark and intermediate races, with reference to the color of the caterpillars. A race in which pigment develops slowly completes the stage appropriate for pigment development before much color is produced, and such a race is pale. More rapid pigment formation produces correspondingly a dark race. An intermediate rate of pigmentation yields caterpillars that are light in the early stages, but dark in the later ones. The speed of development also affects the relative development of male and female organs, but the consequences of this are better set forth in another connection later.

In mice we have already stated that other factors in place of or in addition to natural selection have been sought as possible sources of geographic differences. It was possible formerly, as indicated at the beginning of this chapter, to suppose that the environment might act directly in producing such differences. Since temperature and humidity are the chief factors which fluctuate irregularly, they have been most often considered. Length of day also varies, but changes so steadily from the equator to the poles that no geographic races could be considered to fit it. These factors might be imagined to exert an influence on races in any kind of animal. With respect particularly to mice, the experiments of Sumner showed that temperature had a moderate effect on certain characters. Humidity has been held

by some mammalogists to be the cause of color differences (page 250), but the evidence in support of this conclusion was merely that in general the darker races were in the more humid regions. In the Pacific coast region of the United States, where some of these studies were made, humidity increases from south to north and from the interior to the coast. In this region the color of races was found to darken toward the north and toward the coast. There is no experimental evidence, however, that high humidity directly darkens the hair; and even if there were it would be necessary that the germ cells be affected in like manner to the extent of producing mutations in them in order to get the permanent distinctions between geographic races which Sumner has shown them to possess. Whether the same result might be produced selectively is of course not the question in the present discussion.

Another possibility, that of the action of light working either directly upon the skin or indirectly through the eyes and nervous system, has not been overlooked. It seemed improbable that such an influence might exist but it was tested. In amphibia the color is due to pigment cells in which the colored material can be shifted about. If dark pigment is spread out widely in the cells the animals are dark; if the pigment is closely gathered into small masses the animals are pale. The pigment cells are controlled by the nervous system, and light acting through the eyes may stimulate aggregation or spread of the pigment. Though the pigment in mice does not move about as in amphibia, yet the possibility of its being controlled by light was put to the test experimentally by Sumner. The results showed that no such control exists.

An attempt to unify the basis of varietal differences by connecting them with thyroid characteristics has been made by Yocom and Huestis. They collected two subspecies of *Peromyscus maniculatus* from the different areas in which they live. One, a dark race, lives near the coast, the other is pale and lives in a high desert. After they had been kept in the laboratory for several weeks on the same diet the thyroid glands were examined microscopically. The coast variety was found to have much larger follicles filled with the thyroid secretion than the desert variety had (Fig. 63). Whether a comparison after a much longer period of similar treatment (diet, etc.) would have

shown the same difference is not certain; but a mouse of the dark coastal subspecies which had been kept in the laboratory three years had as large thyroid follicles as those examined more

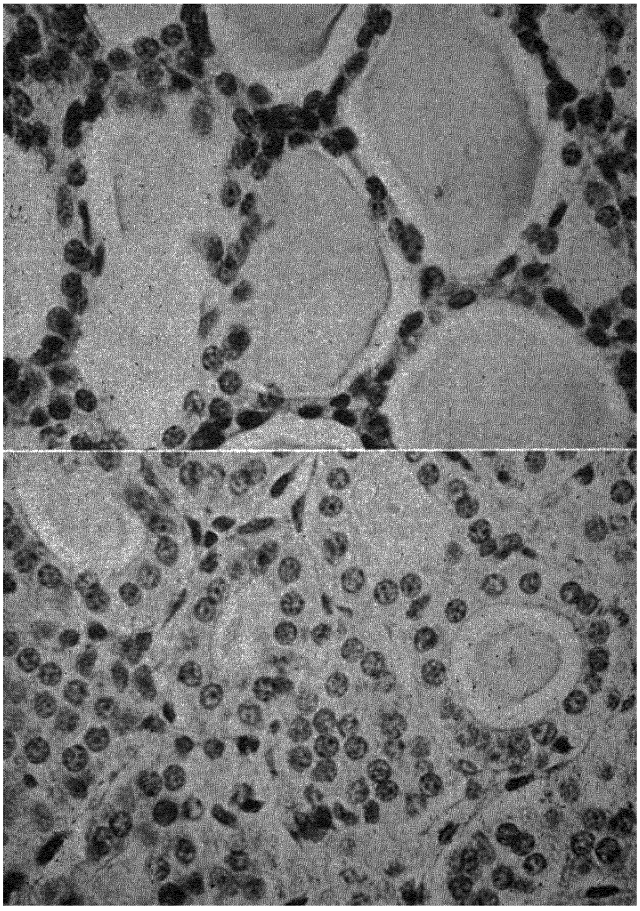


FIG. 63.—Follicles of thyroid gland of deer mouse *Peromyscus maniculatus*. Above, dark coast variety; below, pale desert variety. (*From Yocom and Huestis in Anatomical Record.*)

promptly after collection. Since Sumner's experiments showed subspecific differences in general to be really genetic, it seems warranted to conclude that the thyroid differences were not environmentally produced, but were part of—perhaps the real basis of—the varietal distinctions.

Age of Areal Groups.—How long it has taken races to become separated, or the groups in separate areas to become different, is a mystery in most instances. Naturally their origin must be recent, as time is rated in evolution. It is scarcely possible from the mere facts of distribution to estimate the length of time required in terms of any absolute units. Fortunately an exceptional opportunity to gain knowledge of the speed of varietal change from historical records exists in the studies made of the snail population of certain of the Society Islands. Garrett visited these islands and made extensive collections there in 1860 to 1863, then lived in the islands and continued his studies for many years after 1870. His work was thorough enough to give a fairly complete picture of the snail fauna. Then from 1907 to 1924 Crampton revisited the islands and studied the same areas as Garrett had explored. Crampton reports a number of situations that can only be explained by the assumption that notable changes have come over the snail distribution in the last few decades. Even his own 1924 records no longer fitted the 1907 data in some respects. Species were found occupying much more extensive areas than they covered when Garrett was there. The characteristics of some of them have changed statistically in the same period or since 1907. Two color types of *Partula mooreana* appear to have arisen since Garrett's visit, and there is some degree of geographic separation of them. The species *Partula aurantia*, well established now, was not found at all by Garrett. Indeed, it was not abundant when Crampton first visited the islands in 1907. It has prospered so exceedingly and spread so much since that year that there is every reason to suppose it was practically nonexistent in Garrett's day. One of the varieties of *Partula suturalis* which Garrett found in 1875 to include many sinistral individuals in a certain area, now in the same area is exclusively dextral. In certain areas of this same variety Crampton found fewer sinistral forms in 1923 than in earlier years. These are not isolated instances, Crampton's work is full of them.

It appears, therefore, that in one case at least geographic varieties have formed, and changed, and been replaced by other varieties, not merely within historic times, but within the relatively short period of careful biological exploration, even within the active lifetime of one individual biologist. While not all

races may change so rapidly, it is quite within the bounds of probability that within a century or two considerable changes of these sorts may have come over many of the more rapidly breeding classes of animals.

Transition between Varieties.—When a species is broken up into separated races, how sharply are they distinguished at the borders of the areas? Do the characteristics of one race gradually pass over into those of the other, or are there few intermediates? And does the transformation occur over a wide region, or are the areal limits precisely set? The answer to these questions must depend on the manner in which races become distinct, and the facts of distribution should in turn give evidence regarding that method. Illustrations may as before be confined to species in which important genetic as well as distributional studies have been made.

The gypsy moth races present many intermediates at the borders. These may be, with respect to some of the characters, the heterozygotes produced by crossing. In the case of the sex genes, however, Goldschmidt points out that they may well be pure races possessing intermediate genes. It will be recalled that the sex races are determined by a number of genes (one gene for each race), which Goldschmidt conceives to be merely different quantities of the same thing. As will be seen later, being heterozygous for a "strong" and a "weak" sex gene is apt to result in sterility, while an individual could be homozygous for "intermediate" sex genes and be quite fertile. Since the races are regarded as adaptations to the length of the winter season, an intermediate race in an intermediate region would be quite fitting. In these sex-related characters, therefore, it seems likely that the intermediates are not hybrids of the two types which they separate.

A strikingly sharp separation of two races of mice is that described by Sumner for the deer mouse *Peromyscus polionotus* in Florida and Alabama. The pale variety *albifrons* is found from the gulf coast northward, steadily but very slowly becoming darker, for a distance of about 40 miles. Then in a strip less than 10 miles wide (Fig. 64) it becomes very quickly darker, almost as dark as the dark variety *polionotus*. Indeed, the darker individuals at or near the northern limit of this 10-mile strip would be definitely classified as *polionotus*. Thence inland

for another 50 miles or more the mice are all dark, but become very slowly darker the farther they are from the shore. The 10-mile strip of very rapid change is a puzzling feature. There is no observable feature of the environment which changes rapidly there. The soil inland is dark, while at the shore there is whitish sand, but the 10-mile strip is not one of rapid transition between the two. Sumner dismisses the idea that the two varieties arose separately and have spread until they are just now meeting for the first time. He concedes that they originated separately, the pale *albifrons* coming from a darker type. This pale variety he conceives to have been so favored by the coastal habitat that it multiplied rapidly, and spread because of its own population pressure. It met the darker inland race, probably near their present line of separation, and there was restrained. For some reason as yet unexplained they have not greatly mingled, with the result that the transition is rapid over the 10-mile strip represented in Fig. 64. Unfortunately the genetics of these two races has not been investigated enough to throw light on the problems involved.

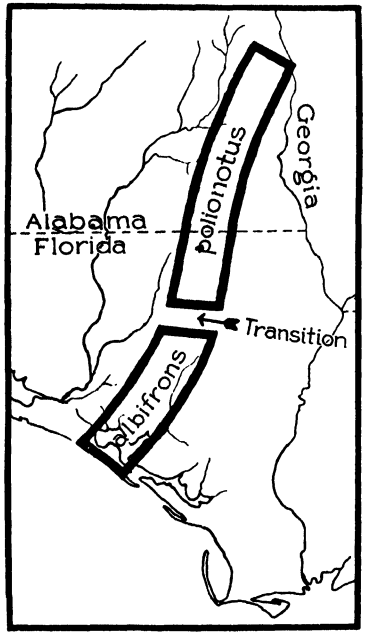


FIG. 64.—Portion of range of deer mouse Peromyscus studied by Sumner, showing sharp transition between the varieties *albifrons* and *polionotus*.

Two varieties of another deer mouse, *Peromyscus maniculatus*, in Montana have been studied by Murie, but since the investigation was more ecological than genetic, their relations are no better understood than are those of the Florida species. One of the Montana varieties is strictly limited to prairie, while the other is almost always in forest. The reason for this separation is only conjectured. In this case there is no area of transition in which intermediate forms are found. Certain measurements were made, that of tail length for example, in which the varieties

differ. The prairie form has a tail averaging 77 mm., the forest form 101 mm. While a mouse with a 90 mm. tail might be assigned to either race, there were almost none of them, and the one or two that were thus intermediate in tail length were not intermediate in any of the other characters. They belonged definitely to one race or the other in all other respects, so that puzzling intermediates were completely lacking.

Are Geographic Races Interfertile?—The merging of geographic races into one another along the common border of their areas is largely bound up with the question of hybridization. Sumner's breeding experiments indicate that in general such races in mice are fertile in crosses and produce fertile hybrids. Notwithstanding such interfertility, the races of *Peromyscus polionotus* in Florida and Alabama, described in the preceding section, showed a very rapid transition from pale to dark color in a very narrow belt between them, as if little crossing occurred. These varieties have been specifically tested for their ability to cross, have done so, and have produced fertile hybrids. Yet if crossing were at all free, a band much wider than ten miles between their areas would be expected to contain the intermediate forms. It seems necessary to assume that crossing which can occur without difficulty in the laboratory does not always do so in nature with the expected freedom. Sumner is much puzzled to assign reasons for the natural failure of hybridization. Psychological barriers to mating, which may be overcome in captivity, are possibilities.

A more extreme separation than the foregoing is that of the prairie and forest forms of *Peromyscus maniculatus* in Montana also described in the preceding section. Murie attributes the lack of intermediates to a complete absence of hybridization, although individuals of the two races must meet where forest merges into prairie. Attempts to cross the two races in the laboratory failed, but this test is not very informative since the forest types did not breed well among themselves in the laboratory. Possibly some dietary requirement for reproduction, such as vitamin E, was lacking in the laboratory regime. Nevertheless, the absence of intermediates is good evidence of lack of crossing in nature. Murie, and before him Osgood, apparently expect to find that these races do cross with one another at other points along their line of contact, or that they indirectly merge

into one another through other varieties. Otherwise they would doubtless regard the two forms as separate species. For the present, however, the types are mere subspecies; and Murie accounts for the lack of crossing at the one place studied by saying that they "simply differ too much to interbreed," thus giving expression to the common view that differences of any kinds, if great enough, will prevent hybridization.

The races of the gypsy moth may be crossed with one another, but from many of the crosses intersexual hybrids result. The reason for this, as explained earlier, is different "strengths" of their sex genes. These genes determine the speed of development of the sex tendencies, so that crosses between "weak" and "strong" races may yield hybrids having improperly balanced embryonic mechanisms. These unbalanced individuals are intersexes, forms more or less intermediate between typical males and females. Since the intersexes are partially or completely sterile, the races which produce them are effectively prevented from giving rise to intermediate hybrid races.

The snails of Moorea must be able to cross when the racial differences concern only color, for snails of different colors are sometimes found in the same broods. These snails carry their young in brood pouches, so that without expensive breeding experiments one can at least ascertain the nature of whole families of individuals. It is inferred from the mixed broods that snails of different color types interbreed. The same freedom appears not to exist with respect to direction of coiling of the shells, for as a rule all members of one brood are alike in this respect; the occasional single exceptions to this rule may be regarded as mutants.

Two of the timothy races having different numbers of chromosomes (42 and 14, respectively) are completely sterile with one another; and two others, the 28-chromosome race in Scotland and the 14-chromosome type in Sweden, cross very rarely, only one hybrid resulting from thousands of cross pollinations artificially made.

Are Varieties Incipient Species?—We are now perhaps as nearly in a position as we shall be in this discussion to answer the question whether geographic varieties are on the way to specieshood. It is clear that such groups of individuals are not in most cases merely responding to the environment in the development

of their distinguishing marks. There are genetic differences between them. Moreover, these genetic differences are not of a fundamentally different order from those that separate species from one another. The geographic placement of the races is sometimes adaptive, sometimes not. Some of the distinctions between such races are of quite recent origin, others are presumably of long standing. Hybridization between races is common, but there are limits to it in some instances.

In the light of these facts, it is a reasonable conclusion that many geographic races are potential species. Most geneticists appear to have adopted this view when they have considered the evolutionary aspects of their subject at all. Goldschmidt, however, rejects the idea completely. To him, geographic types are merely the mutant forms that have been adapted to other areas and have luckily found them. He thinks that geographic varieties have no relation whatever to speciation. Changes that occur within a "harmonious system" may, he concludes, result in such varieties. Only when the changes are so radical as to upset the "system" and destroy the old and establish a new "equilibrium" can a new species be said to have been started. How one should define the quoted words is not clear. The production of intersterility genes could hardly be regarded as upsetting an equilibrium or as destroying an established system. Yet by ordinary standards they, or something else preventing hybridization, are all that are necessary to change local races into species, and something approaching this requirement is already met in a few known instances.

CHAPTER XVII

THE EVOLUTION OF EVOLUTION

> Evolution is not merely change, it is a process of *cumulative* change: fixation in some respects is as important as variation in others.
>
> SEWALL WRIGHT, 1931.

Evolution as described in this book is very closely bound up with the mechanism through which it has to work. Many features of the process must logically be as they are because the mechanism can not work in any other way. It is clear, however, that evolution has not always been of the sort here portrayed, and some of it even at present is not of the type with which we have been dealing. As organisms change, their evolution must change. It will therefore be of interest to set ourselves the problem indicated in the chapter title, of imagining the transformations which types of modification have undergone, but in doing so we shall be fabricating the organisms themselves. This will involve a good deal of conjecture. It would be safer to turn the process about, if the nature of early life were known from any certain testimony. Since, however, the remotest organisms are not known from any direct evidence, we are less likely to forget that we are indulging in pure speculation if we create the supposed mode of evolution and let the living things fit as they will.

The Earliest Organisms.—The first organisms must have been very minute, for any process by which a large living body came into existence out of nonliving matter suddenly could hardly be evolution, it would savor more of creation. What these exceedingly small objects were made of one may conjecture from the most characteristic component of all life at present. All life now is manifested in bodies that are largely protein. There are other organic substances, and some are important; but more of the characteristic behavior of living matter is that of protein substances than of any other. It is to be supposed, therefore, that the earliest animals or plants approached the

proteins in their composition. They were assuredly not cellular in the modern sense. Where they existed is debatable, but there would be more opportunity for their activities in moist situations. They must have had powers of multiplication, and presumably had some means both of maintaining their characteristics and of altering them from time to time.

To what may they be likened at the present time? Duggar and Muller call attention to the small size, comparable to that of genes, of the filtrable viruses, some of them causes of disease in man, which are capable of passing through the pores of the finest filters. These viruses are generally regarded as living objects because of their powers of multiplication. They may be transferred from one animal to another many times, a process which would greatly dilute anything that did not reproduce itself, and yet produce as marked effect in the last animal as in the first one. Clearly the viruses multiply. Mere chemical substances would not thus increase, but living organisms would.

Biologists have not hesitated to go farther and to suggest that the genes of present-day animals and plants may have much in common with both filtrable viruses and the earliest organisms. It is a diverting speculation, with which we may toy without harm, though it must be remembered that all known filtrable viruses live within other organisms, while the first living things could not have done so. If this general line of speculation be followed, it may be supposed that life at first consisted of numerous genes living singly and probably in no particular physical or physiological relation to other genes. It is not meant to imply that any organisms of that time were precisely like any genes of the present. If they only had some chemical similarity, the parallel would have considerable value. And if modern genes were the direct descendants of the early simple organisms, it would not matter how different genes had become, the comparison would be fundamental.

Reproduction and Evolution of First Organisms.—One of the characteristics of protein substances today is the fidelity with which they produce more of themselves. They have a great specificity of action, that is, they behave very definitely and precisely in most respects, and one of the consequences of this quality is the exact duplication of their molecules over and over again. Organisms "reproduce" when they do a comparable

thing and it is presumably their proteins that enable them to do so with so few deviations from type.

The earliest organisms (genes?) may easily have been single molecules, though it is not necessary to any theory of evolution to suppose that they were so simple. Duplication of these molecules, probably in a manner fundamentally like the duplication of protein molecules now, constituted their reproduction. Ordinarily the duplication would be exact, and many organisms identical in composition would exist. They would constitute a species in which there was no variation among individuals, something which does not exist now unless there are equally simple organisms of which we are ignorant. Nothing is known of variability in the filtrable viruses, and the parallel may be fairly close.

Once in a while, just as happens occasionally in proteins now, the production of new molecules would entail a chemical change. A new molecule, a new chemical substance would thus arise, and whether the organisms consisted of but one molecule or many of them, a new type of living thing would exist. When it in turn reproduced, its new form would presumably be continued, and a group of organisms of a new kind would exist. Whether this new group should be called another species is a matter of definition, for our concept of species as they occur in higher animals could not be applied to them. An important feature of species in higher animals is the access which the individuals have to the same stock of genes, and they get this access by interbreeding. Since in the earliest organisms reproduction must have been purely asexual, none of them had any access to genes possessed by any other line of descent. Under these circumstances, any new mutant type which managed to survive might be regarded as founding a new species. If its descendants were not a new species, then an arbitrary judgment would be required to decide how many mutations would have to be accumulated before the new type merited the rank of a separate species. If several differences had to be piled up to make a distinct species, then the species would be connected by intermediate forms differing from them by lesser amounts. Sterility between types could not be used as a criterion of distinctness, since all reproduction was asexual. Such a situation would be—is—maddening in classification of organisms today, and it is just as well no taxonomists lived at that time.

Aggregation of Gene Organisms.—The single-gene organisms may well have accumulated about themselves material which, though living, was of lesser import. Chromosomes today appear to consist in part of "inert" material in which the genes are enclosed, or with which the genes are associated. It is not meant to suggest that this extraneous part of modern chromosomes is like that which collected about the early gene organisms; the parallel is mentioned merely as one reason for supposing that such an accumulation took place.

Perhaps because of this surrounding sheath but possibly for some other reason, the genes may have come to cling together in groups. Whether this aggregation were brought about by the adherence of genes previously entirely separate, or only by the failure of the two genes to separate when a duplication took place, is immaterial so far as the end result is concerned, though the latter is more in keeping with what happens now in the formation of colonies. If aggregates arose only from failure of genes to separate, most such collections would consist of a number of genes of the same kind. Only when the production of a new gene involved some change, that is, only when a mutation occurred, would the aggregation consist of more than one kind. What effect the aggregation would have on the general characteristics of the organism would depend on whether, and how, the genes interacted with one another. Some interaction could scarcely fail to occur, if one may judge from the relation of modern genes to one another.

Reproduction of the Aggregates.—The evolutionary consequences of such aggregation of genes would depend on the manner of their reproduction. If, to reproduce, it were only necessary for the collection to separate into two smaller groups, without duplication of any of the genes at the same time, considerable variation would presumably arise in the progeny. For, if all the genes in one aggregation were of the same kind, the reproduction might separate a large group from a small one, with attendant differences in their properties. And if through previous mutation the aggregation included two or more kinds of genes, reproduction through a random separation of the genes would usually result in two unlike groups.

Such more or less random separation of two groups of genes without duplication of any of them is in keeping with the some-

what irregular manner in which the aggregates are imagined to have arisen in the first place. Multiplication of certain organisms today is to all appearances an irregular or random division of their components. These are the blue-green algae and the bacteria. These cells are without formed nuclei or any other recognizable elements which divide at the time of division of the cell. Things as minute as genes cannot, of course, be seen in them; but the cells possess none of the features which in higher organisms display such a ritual of precision at the time of cell division.

Evolutionary Consequences of Random Separation.—If reproduction of the aggregations of genes were a purely fortuitous occurrence, as just supposed, it would lead to an amount of variation which would be limited only by the number of genes and the number of different kinds of genes in the collection. If an aggregate consisted of six genes, all different, and if reproduction might result in progeny consisting of any number of genes from one to five, then 62 different kinds of aggregations could be produced. If it consisted of seven different genes, and groups of from one to six were possible, there would be 126 different kinds of aggregation. If the reproduction necessarily resulted in the same number of genes in each group, the former aggregation (six different genes) would yield 20 different types, while a seven-gene aggregation could not exist. Even with this latter restriction that each product of reproduction should contain the same number of units, considerable variation would thus be possible.

Any organisms constituted in the way just described would present to the environment many different forms. If even only moderately complicated, they would open a tremendous field for the operation of natural selection. It might be expected that almost any niche of the environment would in time be seized upon by some organism fitted to live in it. Such random reproduction would appear to make possible a very rapid evolution. However, the organisms would not be at all fitted to hold any gains they made. They would lack permanence. Even the fittest for a particular situation would, except by rare accident, give rise to forms not at all suited to the same environment. Any favorable combination would face the prospect of being resolved into unfavorable ones in the next generation. Such

evolution would be entirely foreign to the change so named today. Species now are not only capable of changing, they are capable of maintaining a new constitution. They are slowly modified, but they hold a new form with considerable persistence. They are plastic but not fluid.

It seems unlikely that living things could have long maintained a random mode of reproduction, and yet survived to give rise to the stable species of the present. Their instability was against them. If any among them came, by mutation, to restrict their manner of multiplication, to regularize their division, so that a change favorable enough to survive could be counted upon to be present in succeeding generations, such forms should have been so much better fitted to preserve a foothold once gained that they should have increased through natural selection.

Mitosis the Required Anchor.—The sort of stability needed for the maintenance of advances is furnished in high degree by the chief modern method of cell division, namely, mitosis. The essential features of this mode of multiplication are that each gene in an aggregate is duplicated, and one of the identical genes thus produced goes to each of the new aggregates formed. If such a mechanism, or even an approach to it, could have arisen in the early organisms, then any *individual* that was successful would have an excellent chance to originate a successful *stock*. Gains would be held, while losses would be weeded out as before.

Mitosis has one disadvantage, however, if it is the sole element in reproduction, in that it greatly reduces variation. Aggregations of genes multiplying by mitosis would be only a little more capable of variation than the single genes were before collections of them were formed. Twenty genes might easily have twenty times as great a chance to experience one mutation in a given period of time as one gene has; but the effect of one mutant among 19 unaltered genes, assuming interactions among genes such as occur now, might be very slight. A single mutation could even be without any effect whatever unless accompanied by a given mutation of one of the other genes, and while that other mutation might occasionally arise, it would, as a matter of chance, be much more likely to arise in some individual not containing the first mutant gene. The general result

is that, while mitosis provides stability, it does so more vigorously than is most favorable to evolution. Irregularities might occur at times in this division, but they would usually be so severe as to be disadvantageous or even fatal, as such changes are in cell division now. Doubling the genes without dividing the group of them might produce evolutionary changes comparable to those due to the doubling of chromosome numbers in modern organisms, but such doubling could hardly occur repeatedly. On the whole, the possibilities of evolution with mitosis the mode of reproduction would seem to be strictly limited. Nevertheless, along with occasional change by mutation, it has sufficed to establish a number of kinds of organisms whose only mode of reproduction now, so far as is known, is an equal division or a duplication. It has thus succeeded in moderate degree. Almost certainly, however, the great diversity of modern organisms could never have been attained through so conservative a mechanism as reproduction by simple mitosis with its duplication of genes and the regular segregation of the doubled products.

One of the greatest handicaps to variation in the scheme just outlined was the lack of any means of recombining types of genes already in existence. So long as reproduction could occur only by some sort of fission, each aggregate of genes traced its origin through only one line of descent. It could contain no gene which was not either in that line at its inception or substituted for another gene somewhere along the line by mutation. A combination arose when a mutation occurred, and, if the regularities of mitotic division prevailed in reproduction, it persisted until another mutation occurred.

Recombination through Biparental Reproduction.—This incubus on variation was removed by the adoption of biparental reproduction. What restrictions there were upon this process may be imagined. If any organism were capable of fusing with many other kinds, even with those whose component genes were quite different, the resultant variation would be extremely great. And if in turn the combined product were able to divide in many ways, into parts with variable numbers of genes and without restriction as to which genes went together, the variability would amount almost to chaos. Forms capable of seizing upon every type of environment would be produced, even more certainly than in the supposed unequal and unregulated divisions

before mitosis originated. It seems likely that from the beginning of biparental reproduction there must have been some requirement of similarity of the genes in the uniting organisms. Variability would thus have been reduced considerably, but with freedom in the later divisions of the fusion product it still would have been very great. There could be little permanence of type, little chance of species, under such conditions.

If mitosis occurred in the division of the products of fusion in biparental reproduction, of such a nature that each gene from both parents was duplicated in the process and each offspring received every kind of gene, the only variation introduced by biparental reproduction would be that occasioned by the union of unlike organisms in the first place. If each fusion of two organisms were followed by repeated mitoses of the combined product, something like the permanence of a species might be attained during the period of successive mitotic divisions, but the only variability, aside from occasional mutation, would be that due to the union of diverse parents. Such a scheme might work for a time, but would have one important consequence not yet mentioned. At each union of two parents, the number of genes in the aggregation would be increased—doubled if each parent contributed the same number. If such unions occurred often enough to provide any considerable amount of variation, the size of the organisms would soon become unwieldy.

Meiosis and Restriction of Size.—Increase in size or increase in number of genes due to biparental reproduction is prevented in modern organisms by meiosis, and it is probable that this process arose soon after the introduction of the biparental system. If, as is likely, the parents that could fuse were somewhat similar, particularly if they resembled gene for gene, the product of their union would be made up of pairs of genes. It could then be so arranged that, in biparental reproduction, not all of the genes would unite in the offspring, but only one gene of each kind from each parent. This would require some sort of separation of the similar genes by a scheme that would keep one complete set together. If the original parents did not correspond exactly, gene for gene, their descendants would probably come to do so since any unmatched genes would behave irregularly and eventually be dropped out of the organism. One complete set of genes from one parent would combine with

one complete set from the other parent, and the offspring would consist of a double set just as the parents had done. Repetition of the meiotic process would permit biparental reproduction to go on indefinitely without any increase in the number of genes.

Meiosis and Variability.—This stone of meiosis would also kill a second bird. It would provide additional variation. For the uniting parents, though having *similar* genes, could hardly be expected to have *identical* sets of them. Different mutations in the two ancestral lines would have seen to it that as a rule the parents would differ with respect to some of them. Since in the distribution of genes in meiosis either of the two slightly different genes might be included in a given set, new combinations would constantly arise. The number of these combinations would have a very definite relation to the number of genes in which the parents had differed. An individual having different genes in five of its pairs could make 32 (2^5) different contributions to its various offspring. If the genes of 10 pairs were unlike, 1024 (2^{10}) different collections of genes could be handed on to the several offspring. This source of variability has been described in the chapter dealing with the genetic mechanism of modern animals.

With all these possibilities of variation among individuals it would seem as though organisms had swung too far toward the side of change. It is of small value to organisms to find a suitable environment and then not be able to hold it. One of the advantages of species, that is, of groups of individuals maintaining similar characteristics with but slight change over long periods of time, is that, having come upon a favorable situation, they can occupy it continuously with numbers of individuals. Not so with an organism which possesses little capacity for producing offspring like itself. One of the organisms mentioned above, capable of assembling a thousand or more different collections of genes to hand on to its offspring, and combining with perhaps a thousand different contributions from another individual, would have little chance of begetting offspring just like itself. Probably the offspring would not need to be exactly like the parent, to fit the environment satisfactorily; but almost certainly the bulk of the offspring would fit it less well, and many of them would probably be definitely unsuited. Any scheme by which a favorable combination, once attained,

would tend to be broken up completely in the very next generation, leans too strongly toward the side of variability. This bias would not necessarily be fatal, but success would presumably be greater if there were some brake upon the speed of recombination.

Chromosomes a Conservative Factor.—Some restraint would be imposed on recombination if the genes, instead of acting independently, were collected into groups. This function is served by chromosomes in modern animals. Each such collection would have to contain merely some of the genes contributed by one parent. The other parent in any reproduction would have to match that collection reasonably accurately with another collection of similar genes, in order to have them behave normally in the meiosis of the next generation. That is, if genes 1 to 17 were thus held together in one individual, any individual that cöoperated with it in reproduction would do so most successfully if it too had genes 1 to 17 assembled in one group, though 1 to 19 might work fairly well, or one or two of the genes from 1 to 17 might be missing. Such matching would presumably not be very close at first, but would gradually become better through the elimination of the worst fits.

How much hindrance to recombination chromosomes would offer would depend on how many there were, the fewer of them the greater the restriction. If any animal grouped the genes coming to it from each parent into 8 similar assemblages, so that it had in all 16 chromosomes, and each chromosome differed from its next of kin with respect to at least two genes, that animal could hand on to any one of its offspring any one of 256 (2^8) combinations of genes. The same genes *not* collected into chromosomes would be capable of entering into 65,536 (2^{16}) combinations. This is a very moderate contrast as compared with what might actually happen, for chromosomes differing in more than two genes would be not only possible but highly probable. No matter how many gene differences existed in an individual, if it had only eight pairs of chromosomes it could make only 256 different contributions to its offspring.

It is not easy to say whether this restriction of variation would be wholly desirable or not. It might be in some lines of descent, not in others. It must be remembered that a world of successful life is one in which organisms are able, first, to seize upon the

available situations in the environment, and, second, to hold those situations at least semipermanently. Variation makes the former possible, constancy the latter. It is quite conceivable that the grouping of genes in chromosomes, while helping organisms to hold the places to which they were fitted, left them too little able to adjust themselves to new ones.

Crossing Over.—A still worse feature of chromosomes was that, if they were solidly entrenched groups, certain avenues of change were forever closed. The genes that were assembled in them were together to stay. If genes *A* and *B* existed in several forms each, as *A*, *a*, *a'*, *B*, *b*, *b'*, and *A* happened to be included with *b* at the start of chromosome formation, that combination would persist through the following generations. In other individuals *a* and *b'* might be together, or *A* might be with *b'*, or *a'* with *B*. But whatever combination arose when chromosomes were being formed, that combination would, on the assumption of permanent chromosomes, continue in all descendants of such chromosomes. If no chromosome came to possess both *a'* and *b'* at the outset, the only way to get these two genes into one individual was to introduce them from different parents; and in that case this combination would break up again in the very next generation. In general, much of the evolution which the differences among the genes would make possible is lost if chromosomes, once made, are incapable of reconstruction.

Modern organisms, as we have seen, are not greatly hampered by their chromosomes. For, while these chromosomes possess some stability, they are capable of reorganization. Meiosis, with the preceding close approach of homologous chromosomes to one another, is the instrument which makes this rearrangement of genes possible. Crossing over, or an even exchange of blocks of genes between the pairing chromosomes, occurs to a limited extent. Probably most chromosomes of any size cross over (break) at at least one point prior to each meiosis. Since there are often hundreds of genes in one chromosome, any two adjacent genes may have to wait a long time before their turn comes to separate in crossing over. That is not a rapid way of effecting change, but it has one very important consequence—*every* conceivable combination of genes now becomes possible. Aggregation of genes in chromosomes slows down the process of recombination, but no particular combination is excluded

because it did not happen to arise when chromosomes were being instituted.

When genes began to collect into chromosomes, it is likely that they were held together with very different degrees of obstinacy, just as crossing over now varies in frequency in different stocks. It may be imagined that the looser aggregations were eliminated because they did not lead to the desirable amount of constancy. The more firmly joined groups may have been lost because their descendants were unable to fit into a varying environment. The intermediate strengths of adherence allowed enough variation to fit new or changing environment, but not so much as to destroy the favored types once they arose, and these intermediate ones left more descendants. It is not to be supposed that the higher organisms today exhibit precisely that amount of crossing over which is most favorable to them, for probably some adjustment of that characteristic is still going on. But they are all showing an amount of it which enables them to continue with some degree of success.

Intersterility.—One feature of modern organisms does not seem to be adequately explained by any of the steps yet outlined. That feature is the existence of groups (species) incapable of breeding together with full freedom. Some intersterility would be expected to follow from the necessity of matching the genes contributed by the two parents. Still further restriction of the types that could interbreed must have resulted from the adherence of genes into chromosomes, and the requirement that the chromosomes match moderately well to insure meiosis. It seems quite certain, however, that these two developments could not have produced anything like the amount of intersterility that exists at present. It is known that chromosomes pair even with considerably different genes in them. Also some modern species appear to differ from one another in relatively few of their genes. There would appear to be room, therefore, for much more crossing between different types than actually occurs, if it be supposed that matching of genes and chromosomes is the only requisite to interbreeding.

It is obvious that something has arisen that increases the obstacles to mating or to the production of fertile offspring. Genes which in certain combinations (dominant complements) prevent successful reproduction have been suggested in Chap.

XIV as an adequate explanation of intersterility. Inversions, translocations and duplications are other possibilities, as pointed out before.

Whether intersterility is advantageous or not is debatable. Without it there should be much more intergradation between species than there is. If the environment fell into sharply defined types of habitats, without intergradations, and if living things had succeeded in breaking up into definitely limited species, likewise without intermediates and fitting the various habitats, an ideally adaptive situation would exist. But the environment transforms gradually from place to place in many respects, and graduated forms of life should be able to find accommodation in it. Fortunately, evolution need not be altogether adaptive, even if it dare not be strikingly the reverse. It seems more likely that intersterility belongs mainly to the category of accidental results. The chromosome aberrations suggested above and in an earlier chapter as possible causes of intersterility have every appearance of accidents. Likewise, dominant complementary genes hindering reproduction, if they arise in the same way as other mutations, are to be regarded as accidental in that they are not immediately useful.

Sterility between species is not, therefore, an important means of rendering life more successful. It is, however, a cause of one of the most widespread and most characteristic features of modern organisms, namely, their separation into species and higher groups with few intergrading individuals. The significant consequence of this intersterility is that it permits each line of descent thus isolated from others to go its own way. Each isolated group may thus respond to all the influences of mutation, selection, migration and chance that impinge upon it, without modification or hindrance from the leveling influence of hybridization.

Intersterility almost certainly existed in some form and to some extent from the very beginning of biparental reproduction. It is inconceivable that, of a sudden when some organisms began to fuse in reproduction, all of them should have found themselves capable of doing so. But as the requirements for such fusion changed, the reasons for inability to fuse or to produce fertile products must also have changed. Intersterility has been a progressively different phenomenon as the characteristic features of reproduction altered.

Changes Not Necessarily Serial.—While for the sake of clarity the steps that are imagined to have occurred to change the method of evolution are presented as following one another, they need have done so only in a very general way. There must, of course, have been genes before genes could collect in aggregates. There must have been aggregates of genes before mitosis could have had any meaning. But whether pairing of genes with subsequent meiosis occurred before there were chromosomes or not until later is immaterial. And as stated just above, intersterility was probably no late invention of organisms, though it could have been. The speculative account in this chapter must not be regarded, therefore, as an attempt to fix chronology. It is rather an estimate of the evolutionary significance of the changes which must, some time or other, have occurred.

Persistence versus Variability.—It will be noted that in the evaluation of these several steps some must be regarded as contributions to variability, others must be held to favor the status quo. Genes themselves from the first probably were essentially stable, with only occasional modification. Mutation of the genes constitutes the primary source of variation. Collection of genes into aggregates should have been stabilizing because of its dilution of the effect of a single mutation. But random separation of the members of such an aggregation would provide greater variability. Mitosis aided stability, but meiosis led to variation. Formation of chromosomes helped fix types, but crossing over nullified their effect to some extent. Chromosome aberrations favored variation, partly because the rearrangements directly caused modification of structures, but probably partly also by preventing inbreeding.

Evolution has presumably been all along a mixture of these opposing influences. Many of them have been at work simultaneously. The net result of their operation has been an enormous number of types rather sharply defined from one another, most of them rather stable, but all capable of some change. Within each group, among the higher organisms at least, there is the capacity for interbreeding, so that future generations have access to the genes of all present individuals. These groups have constantly within them the sources of variation, consequently evolution must be expected to continue in all of them. There is no group, not even the highest, in which there is reason to think this evolution has come to an end.

CHAPTER XVIII

EMERGENT EVOLUTION

> Man asks for a specific solution to a complex problem and he is given a verbal sedative. F. S. C. NORTHROP, 1933.

Over a period of years a good deal has been made by some biologists and others of what is called "emergence," as introducing a new, important, and hitherto unutilized element in evolution theory. Since the expression has suffered from meaning, like Paul, "all things to all men," including nothing at all to some of them, it behooves us to consider its significance. The word emergence in this connection seems to trace to the English philosopher G. H. Lewes (Problems of Life and Mind, 1875), who applied it to the results of stimulation leading to subconscious or unconscious processes, which might at any time break in upon the succession of conscious states, and thus "emerge." Among biologists the expression is associated chiefly with the doctrine of C. Lloyd Morgan elaborated in his "Emergent Evolution" in 1923. The essence of the idea existed earlier, however, and has been discussed by others before and since, partly under other names. What is the doctrine involved in all this discussion?

Meaning of Emergence.—As applied to the phenomena of evolution, emergence has generally involved simply new relations. When two physical entities are brought into a physical configuration of which they were never before a part, something new arises out of this relation. Nearly every exposition of emergence has included the example of water emerging out of hydrogen and oxygen. Here are two gases exhibiting the properties of gases in general, and each has some properties peculiar to it. When joined in the pattern of water they give rise to something new—a liquid with properties very different from those of either gas. These properties are said to be emergent. They are the consequence of a new relation between the component parts. Any other chemical compound would serve equally well as an example.

The examples may be pushed backward to more fundamental phenomena, and taken from the formation of the elements out of protons and electrons, let us say. Assuming that once upon a time the elements did not exist (which the psychologist McDougall, in discussing emergent evolution, declines to admit), the electrons and protons must have come together in new relations which resulted in the elements. The properties of these elements were wholly different from those of the component charged particles; their origin was an example of emergence. More complicated illustrations have likewise been used. Proteins, or perhaps better their properties, emerged out of carbon, hydrogen, oxygen, nitrogen, sulfur and phosphorus, none of which had any of the qualities of proteins. Protoplasm with the quality of life emerged out of proteins, carbohydrates, fats, salts, enzymes and water, with properties which none of the components had before they entered into the new relation. Sentience emerged from new relations within living protoplasm, and mind emerged from sentience. The expression "creative synthesis" may be and has been used for essentially the same phenomenon.

In all these concepts there lies the common notion that a whole is something more than and something different from the sum of its parts. This idea has played a considerable role in other biological discussions not related to evolution. Emergence in evolution is but one of the consequences which are held to follow from the establishment of new relations among old entities.

Advantages Claimed for Idea of Emergence.—The uses made of the concept of emergence by biologists, philosophers and moralists have been varied. Jennings greets the new doctrine with fervor, hailing it as the "declaration of independence for biology." The independence he sees biology winning through it is freedom from the restraints of interpretation of the physical sciences. He regards mental qualities as fundamentally different from any other properties possessed by matter, reasons that there must once have been a time when sentience, feelings and ideas did not exist, and concludes that such new things must have "emerged." He even suggests that man acts in some respects on principles different from any which actuate other animals, and these different phenomena must have "emerged." In adopting these views, he decries the mechanist, according to whom mental

states are bound up with physical conditions, and mental processes with physical changes. He goes so far as to say that nowhere is sensation limited to physical conditions which are different from some of those in which sensation does not exist, though it should be obvious that in our present state of knowledge no one can know whether that statement is true or not.

As a result of his inference that mental processes are independent of physical changes, Jennings assumes that conscious thinking plays a role in the determination of events quite apart from any physical processes, thus taking issue squarely with what McDougall terms the essence of modern materialism.

McDougall himself may not be introduced here as an illustration of variance in the use of the idea of emergence, for he does not use it; he rejects it. There is, he says, no emergence in the physical realm, no emergence of sentience out of nonsentience, no emergence of mind out of sentience. Mind is instead an independent type of entity, which has undergone evolution, but has not emerged. For him, any theory of emergent evolution which postulates emergence of mind from the physical realm is faced with an insoluble problem. Yet mind influences behavior, and, as a firm believer in inheritance of acquired characters, he concludes that it thereby influences evolution.

We must not linger, however, over the philosophers' and psychologists' ideas of emergence; they have been well described in McDougall's "Modern Materialism and Emergent Evolution" (1929). The less articulate popular mind has some things to say regarding the advantages of emergence, and to these things we turn. Written expressions of the popular applications are not numerous, but they appear occasionally in antievolution discussions. It appears to be held that emergence makes the evolution pill somewhat easier to swallow, because it paves the way for leaving the quinine of human evolution and the wormwood of kinship of man with the apes out of the prescription. If mentality is something genuinely new and different, and the right idea of emergence be adopted, the higher animals may be set apart from the rest of the living world. And if reason, will and the moral sense are in a real and distinctive sense new, some show of foundation for the thesis that man is set apart from even the higher beasts may be made. Accepting the newness of these mental powers, the popular mind sometimes finds it not

at all difficult to transform the name "creative synthesis" into the shorter expression "creation," and it is held that these higher psychic properties originated by the creation route rather than by evolution. It has thus been postulated that physical man may have evolved, but that psychic man is the result of fiat. Even open minds that do not find the relationship of man to other animals in the least distasteful have sometimes been baffled by the supposed newness of the mental levels, and have wondered how such supposedly radical changes managed to creep into the evolution process. Any one who has frequently discussed the problems of genesis of species with active exploring spirits has doubtless been called upon to offer an explanation of thus getting something out of nothing. The solution of the problem may wait; only the statement of it is here in order.

Still another claim upon the benefits of emergence has been made by the moral philosophers in relation to the doctrines of freedom and responsibility. If psychic properties be held to be but expressions of a material configuration of some sort; if the mental and moral are only consequences of the physical and chemical; then it is easy to assume that the vaunted freedom of the intelligent being is nonexistent and its responsibility for its conduct is zero. The doctrine of the distinctness of the psychic from the physical qualities, coupled with a suitable idea of emergence, makes it quite possible to avoid the despair (also unfortunately the comfort) of fatalism, and to charge the individual with responsibility for his behavior. To adopt this view bestows simultaneously a hope and a burden. To solve for any one the problem whether this conclusion is desirable or not is not within the province of this book; but at least one eminent biologist has jubilantly proclaimed the benefits of the idea of emergent evolution in emancipating mankind from the fetters of the mechanistic concept.

What Is New in Emergence?—If one can decide in his own mind precisely what is new in alleged instances of emergence, he can probably answer—for himself and for others who agree concerning the novelty—the questions that arise concerning the bearing of the whole idea of emergence upon general evolution theory and human conduct. No one seems to have illustrated it with anything new other than the relations into which previously existing things have entered for the first time. Whether

anything else is held to be new is uncertain; if it is, it is vague and ill-defined.

If only the relations of old things are new, let us see what advance we make by postulating emergence. When oxygen and hydrogen first came together in the configuration resulting in water, we are told a new thing emerged. Water has properties which neither component gas has, and these properties are new. Is this newness of a kind which justifies the enunciation of a new principle? There is no indication that the qualities of any fundamental feature of the water have undergone any change. The water may be dissociated into hydrogen and oxygen, and these gases still have their old properties. The nuclei of their atoms are of the same old composition, and the electrons about these nuclei are still of the old sort. These atoms stand ready to unite again under the right circumstances to form water. Why, then, did water emerge from them a first time? Was it because the two gases had never before existed side by side under the conditions which would permit them to unite? Hydrogen and oxygen mixed in a gas container do not spontaneously form water, though they have tremendous possibilities. If these possibilities were never before realized, and water first came into existence when some extrinsic factor was furnished, it is a misnomer to speak of the emergence of the water. The important event was the emergence of the favoring conditions. Doubtless these favoring conditions depended on something else which had not previously existed—some relation between things already long present. These relations in turn depended on some other factor. It is a matter of personal choice whether a name like emergence be applied to any link in this chain of events, but it would be difficult to arrive at any legitimate decision as to which one should receive the name.

The same difficulty arises in connection with every example of emergence. When proteins emerged out of amino acids or more directly out of their constituent elements, only a new relation among old things was produced. There must have been some conditioning factor which was previously lacking, or proteins would have been formed long before. There was presumably a reason why this conditioning factor was not earlier present; it itself was a relation which could not be realized until some

still different circumstance arose. At which of these critical times did proteins emerge? Or was it the proteins that emerged?

In all the proposed instances of emergence about which man knows enough to form a real picture of the thing that is being called by that name it is only a new relation or set of relations cropping out among entities already in existence. Possibly adherents of the emergence idea are willing to subscribe to this statement. They may even wonder why any one should call attention to the fact that it is only new relations of old things that emerge. It is because their conclusions regarding the influence of the concept on scientific theory and human conduct seem to require that emergence be something more than the development of new relations. It is also because their less keenly analytic followers obviously assume that emergence does involve something more than new relations.

Emergence in Evolution.—If emergence amounts only to establishment of new relations, how does knowledge of it modify evolution theory? Some biologists, Nabours, for example, frankly accept new relations of genes as bringing about the emergence of a new character. When the genes for rose comb and pea comb in fowls are first brought together in the same fowl, walnut comb emerges. Neither gene has changed, as is shown by the fact that, when they are separated in different individuals in the next generation, they contribute to the development of the same old rose and pea combs, respectively. Such variations in the products produced by various combinations of genes are endless, as every geneticist knows. Interactions between genes are the general—probably the universal—rule. Change one gene of an interacting group, and the character is changed. Often several characters are changed by a substitution of only one gene. It is not even necessary to have a new combination of genes; merely shifting the position of one or more genes, as by an inversion of a segment of a chromosome, may suffice to modify the character produced. The relation among genes is thus not merely their existence together in the same individual, it is partly their position with respect to one another. And so, if emergence is merely a change of relations among already existing entities, Mendelian heredity furnishes abundant examples of it, and a large amount of evolution for which it was not thought necessary to have a name becomes emergent evolution.

Evolution is not, however, all recombination of old genes. New genes arise by mutation. Is this emergence? If new genes were produced wholly without reference to what existed before, there would be plain justification for regarding them as new. But genes regularly arise from other genes. Just what happens in mutation is not known, but it is almost necessary to suppose that it is a chemical change. In chemical changes new protons, new nuclei, new electrons do not arise. Not even are new elements produced. Chemical change is simply a rearrangement of what was present before, a putting of things into new relations with one another. There is no indication that any mutation is any other than a mere chemical rearrangement.

Intersterility of types, when caused by dominant complementary genes, must originate by mutation. If intersterility is ever due to translocations, inversions or other chromosome aberrations, again it is the outcome of a rearrangement, a setting up of new relations of old entities.

Evolution as a natural phenomenon also includes survival, differential rates of reproduction, and migration. These parts of evolution, however, do not appear to have anything to do with the phenomenon of emergence. No one claims that something new arises when an animal survives amid death on all sides, or when one individual has twice as many descendants as another, or when a group of individuals carrying a mutant gene travels into a neighboring area, though in each of these instances a numerical relation is disturbed, and the new relation might be said to emerge. What is left to be emergent evolution is simply all the rest—the primary part and one of the secondary parts—of evolution, the mutation and recombination of genes. Thus, evolution in general is as emergent as any part of it can be proved to be. It would be difficult to maintain that out of all the discussion started by Lloyd Morgan anything had emerged except a new name for an old phenomenon.

If, after all, emergent entities are not merely new relations, if they belong to entirely new categories, then emergent evolution needs to be redefined by its sponsors. Illustrations drawn from chemical compounds must be abandoned, unless it be supposed, for example, that prior to the formation of water hydrogen and oxygen could be and probably were brought together under circumstances which later would have caused

them to unite, and yet water was not at that earlier time produced. If life is due to something else, and more, than new relations, that point should be made clear by the emergentists. If sentience, and later mind, are supposed to depend on something categorically new, not just on new relations between old things, that claim should be unequivocally made. If supporters of emergent evolution are claiming only that it consists of new relations, their readers are persistently interpreting it to mean something more. The doctrine, batlike, is fighting under two flags; for the sake of progress it should renounce one and remain loyal to the other. If that is candidly done the theory will be promptly assigned its correct place in scientific philosophy.

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