

lection. From the law of ancestral heredity Pearson has calculated the probable effect of perfectly rigorous artificial selection. His results are given in a table, from which it is possible to calculate the curves of six successive generations where the parents selected have a given deviation from the original mean of the population. Fig. 1950 illustrates such a case, where the mean of the population is represented by  $M = 0$ , the standard deviation is  $\sigma = 1$ , and the parents for each generation are supposed to have the selected character of the value  $H = +2$ , or twice the standard deviation. Then the average deviation of the first, second, third, etc., generations of offspring from the original mean of the population will be represented by the distance from  $M$  to the ordinates  $h_1, h_2, h_3$ , etc. It will be seen that the regression becomes less in each generation until, in the sixth,  $h_6$  almost coincides with  $H$ . In other words, if it were possible to make this rigorous selection, we might expect at the end of the sixth generation to obtain a new race that would breed true about a mean differing very little from the selected value.

Turning now from *a priori* considerations to observed facts, what evidence is there that natural selection has actually been a factor in evolution?

First, there is the observed fact of a selective death rate. To say that where the death rate depends upon individual peculiarities the fittest will survive in the struggle for existence, is a truism, for our only means of judging of fitness is the ability to survive. While a great deal has been written upon the subject, exact observations have only just begun to be made. It is not often easy to find a correlation between structure and the death rate. Only two instances are on record.

From measurements made by Thompson and himself in successive years, Professor Weldon came to the conclusion that in the crabs, *Carcinus maenas*, in Plymouth Harbor, England, the frontal breadth of the carapace was becoming narrower from year to year. Seeking a cause for this he found it to be probably the increase of sediment in the harbor, due to the building of a breakwater, which hinders the flow of the tides. To test this theory, he placed a number of crabs in aquaria with a considerable quantity of china clay, like the silt in the harbor, suspended in the water. A number of crabs died, and at the end of the experiment the dead crabs were separated from the living, and all were measured. It was found that the survivors had distinctly less frontal breadth than the dead crabs.

If this selective destruction is continually going on in the harbor, then the crabs protected from the action of the silt during a portion of their lives should show a greater average frontal breadth than the wild crabs of the same age. A number of crabs were kept in aquaria with clean sea-water until they moulted. When the shell was hard they were killed and compared with wild crabs of the same age. It was found, as expected, that the frontal breadth of the protected crabs was greater.

The great storm of February, 1898, enabled Bumpus to study a similar case among the house sparrows (*Passer domesticus*). During the storm in Providence 136 birds were picked up in a helpless condition. When brought into the laboratory 72 of these revived and 64 died. A number of measurements were made upon each bird of the two lots, and it was found that the mean of surviving birds differed perceptibly in many dimensions from the corresponding mean of the dead ones. Moreover, the dead birds showed a greater average deviation from the mean than the surviving ones.

In these cases single characters were studied in relation to the death rate. It would be more to the point if we could correlate the sum of the peculiarities of the individual as a whole with his chances of death, for natural selection acts upon whole individuals, not upon single characters. Pearson has demonstrated a very ingenious method of doing this for man. If there were no natural selection, the whole death rate would be non-selective, fortuitous; on the other hand, natural selection would reach its maximum efficiency when the death rate becomes wholly se-

lective. In nature the death rate would be usually partly selective and partly non-selective, and the problem is to determine what proportion of the total death rate is selective. In Pearson's method "no attempt is made to select any particular organ, but we take pairs of individuals having some general resemblance in their whole complex of organs and characters, and correlate their fitness for surviving under practically the same conditions of life. Now pairs of relatives or members of the same family are precisely such individuals. If there were no selective death rate there would be no correlation between the ages at death of, say, brothers. On the other hand, if there were no non-selective death rate we might reasonably suppose duration of life would be determined by the law of ancestral heredity," and we should expect the correlation between the durations of life of pairs of brothers to be the same as that observed in the case of stature and other characters.

From a study of one thousand pairs of brothers recorded in the pedigree Pearson found that of the total death rate eighty per cent. was selective. Comparing fathers and sons, the result was sixty-five per cent. Natural selection, then, is by no means inoperative at the present time in the human species.

The second line of evidence is one that especially meets the objections of the advocates of the theory of special creation. This is that it is impossible to find throughout the whole range of the animal and vegetable kingdoms a single structure or function developed in one species for the exclusive benefit of another.

Darwin regarded this point as of so great importance that he offered to give up his whole theory if it could be proved in a single case that a structure or instinct is developed in one species for the exclusive benefit of another. To be sure, there are innumerable cases in which the characters of one species are of use to another; but this value to the other species is purely secondary. For example, the nectar of flowers forms the daily food of bees, but this nectar is primarily of use to the plant in securing the visits of the bees, and thus providing a means for the transportation of the pollen and cross fertilization. As the result of thoughtful search Romanes was able to discover only two cases that appear to be exceptions to

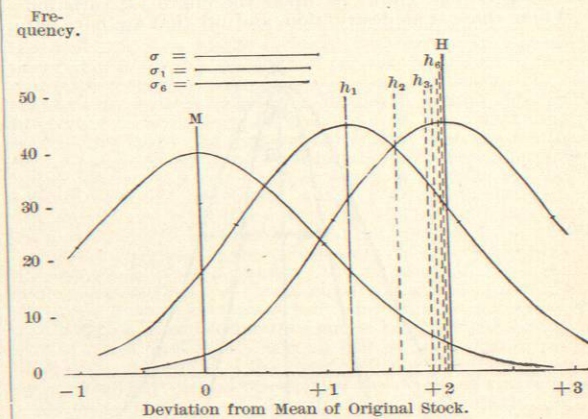


FIG. 1950.—The effect of a rigorous artificial selection during six generations, where the selected parents of each generation deviate from the mean ( $M$ ) of the original stock by twice its standard deviation ( $H$ ). The broken lines  $h_1, h_2, h_3, \dots, h_6$  represent the position of the means of the first, second, . . . and sixth generation of offspring. When  $M = 0$  and  $H = 2$ ,  $h_1 = 1.2$ ,  $h_2 = 1.6$ ,  $h_3 = 1.85$ ,  $h_4 = 1.90$ ,  $h_5 = 1.94$ ,  $h_6 = 1.97$ . The curves of frequency are drawn for only  $M$ ,  $h_1$  and  $h_6$ , and their standard deviations are  $\sigma = 1.0000$ ,  $\sigma_1 = 0.9555$ ,  $\sigma_6 = 0.8944$ . (Data from Pearson.)

this rule. It is well known that the aphides (green plant lice) secrete a sweet juice that is much sought after by ants. So far as we know, this secretion is of no value to the aphid. But it has not yet been investigated suffi-

ciently to show that it is of no use. It may be a means of removing waste products of metabolism. Moreover, it seems to be rather more of a luxury than a necessity for the ants. The other case is still more remarkable. It is the production of galls upon plants as the result of the growth of an insect larva within the tissues of the plant. The gall forms a perfect home for the larva, and differs in character, not only in different plants, but it differs also according as it is produced by one species of insect or by another, each species of insect having its own peculiar form of gall. All grades are found, from simple cysts, hardly worthy to be called galls, to structures which are extremely elaborate. Here we have a structure developed by a plant apparently for the benefit of an insect. But, as pointed out by Romanes, the gall arises as a reaction on the part of the plant to a poison produced by the insect, and its first appearance was probably due to one of those accidental effects of an injurious substance upon an organism, such as Herbst discovered when he treated sea-urchin larvae with potassium and lithium salts. The gall-forming property, being of use to the insect, would be preserved and modified by natural selection acting directly upon the insect, and the plant would be affected indirectly.

The third line of evidence is that which first attracted Darwin's attention to the principle of selection. Darwin found that in the production of domestic varieties of animals and plants artificial selection is the keynote to success. All of our domestic productions are descendants from wild species, but in many cases either the wild parent species has been exterminated, or else the domesticated descendants have been so greatly modified that it is impossible to recognize the ancestral form. The differences between artificial varieties and between them and the original form, when known, are often as great as the differences between species, or even between genera, of animals and plants in the natural state. Compare a deer hound with a King Charles spaniel, a Cochin China with a game cock, a pouter pigeon, a fan-tail, and the wild rock dove, from which Darwin showed the pigeons to be descended. Romanes calls special attention to the well-marked varieties of canary birds, and regards this as a case of unusual interest because of the shortness of time during which the evolution has taken place, the first mention of these birds that he could find being by Gesau in the sixteenth century. Among most of our domestic animals man has been selecting more or less unconsciously the individuals which best served his needs or answered to his ideal of beauty; and this has been going on since prehistoric times. In later years selection has been practised with great care and with reference to more exact ideals, and the progress made is truly wonderful.

Darwin regarded evolution as an extremely slow process, and this idea prevailed for a long time, but recently several cases of very marked change in domestic forms have come to light where the change has been comparatively rapid. The American trotting horse is a case in point. An ordinary horse runs when he wants to move rapidly, but the trotting horse prefers the trot, and will keep to that gait until he attains a speed far beyond that at which other horses would be forced to break into a gallop. The lowest limit of what is regarded as racing speed in a trotting horse is a mile in two minutes and thirty seconds. The first horse to make a mile within 2:30 was Lady Suffolk, a great-granddaughter (by three crosses) of Messenger, a thoroughbred race horse imported from England in 1788, and famous as the ancestor of almost all American trotting horses. Lady Suffolk was foaled in 1833, and made her record in 1845. From that time the speed of the fastest trotter has steadily increased, until Cresceus, foaled in 1894, made the remarkable record of 2:02½ in 1901, beating the record made by The Abbot the previous year. But the improvement of the trotting horse is seen best when we compare the number of fast trotters at a recent date with the number several years before. In 1892 there were 116 horses with records of 2:15 or better, at the end of 1897 there were 585 horses with such records, and during 1897 109 horses entered

this class, only 7 less than the total number in 1892, and many of these had no previous record.

Now is this improvement due to the selection of fortuitous congenital variations, or to some other cause? If races are changed by the inheritance of acquired characters, this process should be expected to be efficient in the case of the trotting horse. This question will be discussed later when we consider the inheritance of acquired characters as a factor of evolution. But it may be said now that, of the sixteen champion trotters from Lady Suffolk to Cresceus, Cresceus is the only one having a sire with a record below 2:30, and The Abbot is the only one that has a dam with any record at all, and it seems probable that a careful study of the pedigrees of trotting horses will fail to show that horses which have been trained have any greater power of transmitting trotting speed than horses which have not been trained. It is probable that such a study will show that that combination of instinct and structure which enables a horse to trot at a high speed has arisen as a fortuitous variation in a few individuals, and that fortunate selection and crossing of their descendants during eight or ten generations at most has produced the remarkable result that we see to-day. This is the more probable since Galton has shown that variations in speed follow the normal curve. Take the pedigree of Alix, for example. Both parents of this champion trotter were totally untrained. Her paternal grandsire has a record of 2:21¼, the others have no record. Of her grandparents only one has a record (2:21¼), and of her great-grandparents again only one has a record (2:42). On the other hand, her descent is traced by more than fourteen converging lines from Messenger, the ancestor of Lady Suffolk. She is descended by four lines from imported Bellfounder, the son of a Norfolk trotter, and by four lines from Amazonia, a "natural trotter." Moreover, she counts among her ancestors the sires of three champion trotters: Dexter, 2:17¼; Goldsmith Maid, 2:14, and Maud S., 2:08¼, and if each ancestor be regarded as a separate individual at each place in which he occurs in her pedigree, it will be found that she is descended from seven sires of champions, three on the paternal side, and four on the maternal side.

But if the inheritance of acquired characters may be a factor in the development of the trotting horse, there are other cases of rapid improvement in which it cannot have entered. One of these, the cultivated cyclamen (*Cyclamen latifolium* Sibth.), is one of the spring wild flowers in Greece and Syria. It has pink flowers with a ring of darker color at the throat (W. T. Dyer, *Nature*, May 20th, 1897, vol. lvi., pp. 65-68). The species is said to have been first cultivated in Europe at Lille in 1731. It was probably obtained from Syria. "The Lille plant ultimately went to Ghent, and it has been asserted that all the cultivated forms in existence are descendants from this one individual." A variety with white flowers—"pure white with a bright purple button"—was described in 1768. The modern development of the plant began in 1860, and started with one of the principal growers (Messrs. Sutton) with the old "crimson and white."

The changes have been brought about entirely without resort to hybridization. But starting with the slightest deviation, even so small as the slightest difference in a cotyledon of a germinating seed, by careful self-fertilization and selection the present varieties have been produced. The changes produced have been in the size of the flower, its fragrance, color, and form of corolla. The original form has narrow, twisted, reflexed petals about an inch long. The cultivated varieties have broader, less twisted petals, and in one variety they have reached a length of three inches. This was accomplished by continuous in-breeding and selection. The old crimson and white had a crimson ring at the throat, but was otherwise an albino. From this, forms have been produced varying from pure white, on the one hand, to a uniform deep crimson, on the other. "The modern colored forms were obtained in the first instance by selecting forms in which

the colored ring showed a disposition to spread into the white corolla segments. The first indication would be a scarcely perceptible streak. By selection from self-fertilized plants the streak was widened into a stripe. Continuing the process, the stripes united, and a uniformly colored flower was obtained." The colored varieties when self-fertilized come true from seed.

One of the most remarkable modifications in the form of the corolla is the spreading of the segments. Cyclamen belongs to the order *Primulaceae*, and is distinguished from the rest of the tribe *Lysimachiae*, to which it belongs, by the reflexed segments of the corolla. In the variety with a spreading corolla, then, we see a modification of a character which not only distinguishes the species but also the genus.

Doubling has occurred in one variety. Ordinarily doubling is due to a homœotic variation of the stamens by which they become petal-like. In this case, on the other hand, the stamens retain their proper structure, and both they and the segments of the corolla become increased in number.

The butterfly form is a case of parallel variation, it having been obtained independently by several horticulturists. In this variety the petals are partly spreading and arched, and are toothed and curled at the edges. It is interesting to note that in one case at least there is a correlation between the corolla and the leaves, for they also are toothed. This variety arose as a well-marked sport which was improved by selection.

Another example of the rapid effect of selection is the tomato. The different varieties of the edible tomato (*Lycopersicon esculentum*) differ as much, if not more, than do the other species of the genus (Bailey, "Survival of the Unlike," pp. 112-125). Colonel Waring, who introduced the Trophy tomato in 1872, gives the history of this variety, from which the best modern tomatoes have been produced. The Trophy tomato was the result of crossing and selection begun by Dr. Hand, of Baltimore County, Md., in 1850. He began by crossing the smooth "Love Apple," which was filled with juice and seeds, with the common convoluted red tomato of that period, which was so rough as to be unfit for use. It consisted practically of four or five separate fruits packed together in one, with the skin running far into the convolutions. After several years by continued in-breeding and selection he succeeded in producing a form which combined with the smooth skin of the Love Apple the solid fleshy mass of the compound red. This accomplished, he continued to select a very few specimens of the best and best flavored of the earliest fruit for the next year's seed, and thus increased the size and solidity of the fruit, until in 1870 he had produced a variety which was a mass of flesh interspersed with ten or more small seed cells, and which was the earliest, largest, smoothest, the most fleshy, and much the best flavored of all the kinds then grown. Moreover, the continued selection had resulted in a marked fixity of type, which was very different from the two- or three-celled original form.

The growth of sea-island cotton, on the islands off the coast of South Carolina and Georgia, was made possible only by the process of selection. When first introduced from the West Indies, the plants were not adapted to the climate, and seldom produced fruit. But by rigorous selection a race was produced which was well adapted to the climate, and the quality of the fibre was improved until now it is the best grown in any part of the world. That the improvement in the fibre is due to selection and not to conditions of growth is shown by the fact that when selection is relaxed the fibre deteriorates (Webber, "Year-Book Dept. Agric.," 1898, p. 358).

Many more examples might be cited to show how great the changes are that have been produced by artificial selection. Many domestic races produced in this way differ as much from each other and from the parent species as do species or even genera in nature. If artificial selection acting during only a few generations can produce so great changes, how much more effective must have been natural selection, which is probably

much more rigorous and continuous, acting through countless ages.

To sum up, then, we have considered three lines of evidence that natural selection is a factor in organic evolution: 1. We have observed facts of the struggle for existence and a selective death rate. 2. We find that no organism in nature has developed any structure or function for the exclusive benefit of another species, contrary to what we might expect to find on the theory of special creation; but just what must be the case on the theory of natural selection. (This would probably be true also on any theory of evolution.) 3. We find that the analogous process of artificial selection has been the most effective means of developing in domestic races those qualities of most value to man, and therefore we infer that natural selection has been an important factor in developing in natural species those qualities of benefit to themselves.

One of the best ways of testing a theory is to attempt to apply it to concrete cases of the class of phenomena which it is supposed to explain. In the applications of the theory of natural selection we shall find the fourth and last line of evidence in favor of the theory.

The phenomena in question are in general those of adaptation. Many plants have especial floral structures which facilitate cross fertilization by the aid of insects, and Darwin has shown that this is of great advantage to the species. Climbing plants have peculiar structures and powers of movement that are clearly of advantage in enabling the long, slender stems to find support. Both plants and animals frequently have structures which serve to repel enemies, and many animals are provided with a protective coloring which renders them inconspicuous to their enemies or to their prey. Other animals, provided with offensive secretions or weapons, also have conspicuous warning colors which render them less liable to attack. Finally, there are inoffensive animals which resemble the offensive ones superficially in color and form, and by this mimicry probably share in their immunity from enemies.

These are examples of a large and important class of phenomena that, rejecting the theory of special creation, can be explained by only one theory of evolution, that is the theory of natural selection. Thus we see that natural selection is not merely a factor, but is perhaps the most important of all factors in organic evolution.

Passing over the objections to the theory of natural selection that arise from misunderstanding of the theory or ignorance of the facts, there are three objections that are important.

First, it is true that a great many species are distinguished by differences of form or color that are so minute that it seems impossible for them to be of selective value. Not knowing all the conditions of life, we are unable to say that such differences are not in themselves of selective value or correlated with characters of selective value. But in many cases there is no evidence of such value or correlation.

Second, one of the most marked peculiarities of species is infertility when crossed with other forms. Now it is difficult to see how infertility of any form could be produced by natural selection, except in relation to the food supply. But food supply could have nothing to do with infertility between species.

Third, a distinction must be drawn between linear evolution and divergent evolution. Linear evolution would be the gradual change of specific type by which the new species would become different from the old, but the number of species would remain the same. Divergent evolution, on the other hand, would mean the splitting of original specific types into two or more new types. Now it would be impossible for a species to become multimodal and ultimately to separate into two or more by the action of natural selection alone. For there would be nothing to prevent individuals of different types from breeding together and thus reducing them all to a common type.

These objections are valid, unless some other factor

may be brought to the aid of natural selection. But selection is not the only means employed by the breeder of domestic races; then why should natural selection be supposed to be the sole factor of organic evolution?

Isolation.—When a breeder wishes to improve a race or to create a new one, he not only makes a very careful selection of his breeding stock, but he builds a fence around it and guards it against admixture with other stock. That this principle of isolation, or segregation, is of great importance as a factor of organic evolution has been pointed out, especially by Gulick and Romanes. By isolation is meant "simply the prevention of intercrossing between a separated section of a species or kind and the rest of that species or kind." Romanes regards natural selection as a prime factor of vast importance in evolution, but he believes it to be less fundamental and of more limited application than the principle of isolation. He says: "Equalled only in its importance by the two basic principles of heredity and variation, this principle of isolation constitutes the third pillar of a tripod upon which is reared the whole superstructure of organic evolution."

From this point of view natural selection becomes a special case of isolation, where the individuals best fitted for their environment are isolated and prevented from crossing with inferior individuals by the death of the latter. But, as we have seen, this form of isolation can produce only linear, or monotypic, evolution, for of the two separated sections of the species only one survives. It is possible, however, that the modal type might become the least favorable, and that selection would result in the separation of two types equally fit. To borrow an illustration from Pearson, suppose a short femur and a long radius to be equally favorable and their combination in one individual so rare as to be negligible. Rigorous selection would produce two pure types, as in Fig. 1951, I. But natural selection alone is powerless to prevent the free intercrossing of these types, and the birth curve of the next generation will have the form of II in Fig. 1951. Selection will need to be repeated with equal rigor, otherwise in the third generation we shall find an approach to the normal curve with the mixed type as the mode, six times as numerous as either pure type (Fig. 1951, III). By natural selection alone, then, we should have in such a case merely periodic selection and no progress in divergent evolution. In order that the types A and B may become the foundation for two new species, some other barrier must arise between them. We must look for some other form of isolation.

Isolation may be total or it may be partial of various degrees. A more important distinction is between isolation that is "discriminate" and that which is "indiscriminate." Indiscriminate isolation allows free intercrossing of all variations, or *apogamy*; while discriminate isolation allows only individuals having some point of resemblance to breed together, or *homogamy*.

Apogamy will occur only where sections of the species contain large numbers of individuals at the time of separation. In this case there will be no change of type unless the separated sections become subjected to different conditions so that natural selection may act in a different manner.

Where the isolated section is so small as not to be a fair sample of the population, there will be a sudden

change of type. That is, the mean of this section will differ somewhat from the mean of the species as a whole, and there will be a certain degree of homogamy. But this change of type may be very small, and it is very doubtful if homogamy without natural selection can produce any continuous change of type, although Gulick and Romanes have held that it can.

Geographical isolation has, without doubt, played a very important part in the differentiation of species. As we have seen, it will give rise to homogamy or apogamy, according to the number of individuals separated. But probably its most important effect has been to allow the gradual adaptation of parts of a species to different conditions, which would be impossible where free intercrossing could take place.

There are numerous forms of homogamy. "When, for example, any section of a species adopts somewhat different habits of life, or occupies a somewhat different station in the economy of nature, homogamy arises in

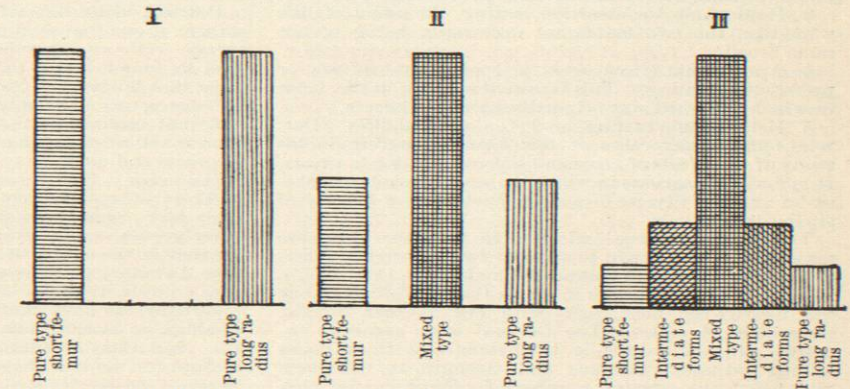


Fig. 1951.—Illustration of the Swamping Effect of Inter-crossing. I, First generation—selection intense, modal type destroyed leaving two pure types distinctly differentiated; II, Second generation—random mating of the two pure types of equal fertility. Results, mixed type twice as numerous as either pure type. III, Third generation—random mating of the second; all individuals equally fertile. Results, mixed type six times as numerous, and intermediate forms four times as numerous, as either pure type. (Data from Pearson.)

that section." In plants differences in times of flowering, in habitat, or in the habits of insect visitors may give rise to homogamy. But, according to Romanes, aside from natural selection, the most important form of homogamy is sexual incompatibility, which he calls physiological isolation. In this form of isolation individuals having some peculiarity of the reproductive organs are prevented by this from crossing with individuals having some other peculiarity. If this sterility between different sections of the species be correlated with other peculiarities, we have what Romanes calls *physiological selection* and the formation of a new race, which is free to develop independently of the rest of the species.

This theory is based upon two principal considerations: (1) the general variability of organisms, including the reproductive organs, and (2) the fact that the character that chiefly distinguishes species from varieties is sterility between them. This sterility may be absolute, or it may result in the production of more or less sterile hybrids. Whether sterility has arisen before or after other divergent characters, it will be, in either event, an important factor in evolution. We must suppose it to have arisen gradually and to have spread until it affected a number of individuals; but it is difficult to see how this could have taken place without the aid of some other form of isolation.

The chief evidence for the theory of Physiological Selection is found in the topographical distribution of plants. Naegeli found ninety-five per cent. of allied species and a great number of allied varieties living together

in the same stations separated by no barrier except sterility. And this is confirmed by the experiments of Alexis Jordan, published in 1873. He discovered in plants great numbers of varieties hitherto overlooked owing to the minuteness of the differences between them. And he found that in many hundreds of cases these varieties, in nature living side by side, would breed true to seed and be sterile *inter se*.

**Sexual Selection.**—Another series of special cases of isolation is furnished by the various kinds of sexual selection. This term, as recently employed by Pearson, includes all forms of *selective mating*. This is sharply contrasted with *panmictic mating*, or the mating at random of all members of the race. The forms of selective mating are classified by Pearson as follows:

1. Autogamic mating, or self-fertilization, including the fertilization of a flower by another flower on the same plant.
2. Endogamic mating, or mating within the family, brood, or clan, a very effective mode of isolation.
3. Homogamic, or assortive mating, the union of like with like, the two mates not necessarily being of the same brood.
4. Apolegamic (from *ἀπολέγω*, I pick out, refuse), or preferential mating. This is *sexual selection* in the sense in which the word was originally used by Darwin.
5. Heterogamic mating, or the union of unlikes. Darwin found many cases of this form of mating in his study of the effects of cross and self-fertilization in plants. It includes those cases in which the species is polymorphic and a union of diverse forms is prepotent over a union of similar individuals.

The theory of sexual selection in the narrower sense was devised by Darwin to account for the origin of certain secondary sexual characters in animals.

There are many species in which the individuals of one sex, usually the male, fight with one another for the possession of mates. The fur seal is an excellent example. In such cases it is obvious that those males having superior weapons and strength to use them will beget the greater number of offspring, and that these will inherit and transmit their favorable peculiarities. This might be regarded as a special form of natural selection.

But there are many species, especially among the birds, in which the contest for mates is carried on by gentler means. In these cases the males usually seem to vie with one another in an attempt to excite the sexual instincts of the females by melodious song and cries, by movements of the body, or display of bright colors. It is supposed that those males which are most attractive to the females will produce the most offspring, and thus the development of ornamental secondary sexual characters is regarded as due to selective action on the part of the females.

Of course, this theory can apply only to animals of a relatively high grade of organization, and the efficiency of this factor in evolution has been denied entirely by Wallace and others.

To enter into this controversy would require too much space. But it may be pointed out here that (1) males are frequently distinguished, not only by bright colors, but by a highly decorative color pattern, sometimes associated with a highly elaborate structure, as in the peacock, angus pheasant, bird of paradise, etc.; (2) many birds possess not only call notes, but a melodious song, often to our ears, at least, of great beauty, as the wood thrush, the wren, and the catbird; (3) and, finally, the deer family possess handsome arborescent antlers that are highly ornamental, but certainly less efficient weapons than the straight horns of the antelopes. Now these facts cannot be explained by the assumption of vigor of the male, nor by the usual process of natural selection, while they are easily explained on the theory of preferential mating.

In order that the choice of the female may be an efficient factor in evolution there must be a certain general tendency in one direction. In order to discover whether

this be true or not it would be necessary to resort to careful statistical inquiry.

Pearson has pointed out the method for making such inquiries, and in the case of man he found no evidence of preferential mating in respect to stature, but he found distinct evidence of preferential mating in the matter of eye-color or of some closely allied character in the male. The general tendency is for the lighter-eyed to mate, while the dark-eyed are less frequently mated. He concludes that it cannot be doubted "that sexual selection in the form of preferential mating is not a mere hypothesis, but can be demonstrated to actually exist in the case of man."

Preferential mating would have an effect on evolution similar to that of natural selection. That is, there might be a tendency to progressive change of type, but it could not alone produce differentiation. On the other hand, it is clear that self-fertilization and endogamy would aid differentiation, and assortive mating would also have this effect, if mating of this kind takes place.

Pearson, using the method of correlation, studied the stature of one thousand pairs of husbands and wives, and the eye color of seven hundred and seventy-four pairs. And he found that, "the assortive mating is indeed so great that husband and wife have for the average of these two characters a sensibly greater degree of resemblance than that assumed on theoretical grounds to hold for first cousins and approaching the degree of resemblance found for uncle and niece."

**Panmixia.**—The presence of vestigial organs in vast numbers of species, and the fact that some groups entirely lack organs possessed by other related and perhaps lower groups, as, for example, the snakes, lead to the belief that in the course of evolution organs in many cases have dwindled in successive generations, and sometimes have entirely disappeared.

Perhaps the most natural explanation of these facts would be to ascribe them to the inherited effects of disuse. But this explanation is inadequate, for it will not account for the loss of parts in plants, nor for the loss of passively protective structures in animals; and it is particularly inapplicable to the cases of the loss of wings in neuter insects, for neuters produce no young, and hence there could be no inherited effect.

To meet this difficulty Weismann introduced the hypothesis of *panmixia*. This is merely random mating without selection. But, as has been pointed out by C. L. Morgan and Pearson, the only effect of panmixia would be a reduction from the survival mean to the birth mean. There would be a sudden slight change of adult type in one generation, and after that no further effect.

So it would seem that we must fall back upon Darwin's principle of natural selection and economy of growth. For example, in the case of wingless insects inhabiting small oceanic islands, it is evident that if the species were unable to become strong fliers, it were better for them not to fly at all. Because weak fliers would be apt to be blown out to sea and lost. Darwin argued also that useless organs require as much nourishment as useful ones, and in time of dearth the animal which had to find nutrition for the smallest amount of useless tissue would stand the best chance of surviving. This might account for the dwindling of useless organs, but it would not account for their complete disappearance. For it cannot be supposed that the presence or absence of a minute vestige of an organ could ever be a matter of life or death. And as no satisfactory hypothesis has been advanced to explain this, we shall have to regard it as one of the unsolved problems of evolution.

**Bathmic Evolution.**—Paleontologists have asserted that they find in the study of extinct animals evidence of a constitutional tendency toward variation in a definite direction. Such a change of type, due solely to something inherent in the constitution, without action of organic or inorganic environment, is called *bathmic* evolution (from *βαθμικός*, basal).

The evidence that such evolution has taken place is not very convincing. Nevertheless, supposing it to be a

fact, many explanations have been offered to account for it. Mivart suggested an innate tendency, and Naegeli, a perfecting principle. But these are merely words and explain nothing. Hyatt from a study of certain fossil mollusca, ammonites, found evidence of a cycle of development of species corresponding to the cycle of individual development. He holds that there is a law of growth which compels species to pass through the stages of youth, maturity, and senescence. This may be true of the ammonites; it may be the reason that they are extinct. But it has not been shown to hold for any other group, and the law itself would need explanation.

Weismann has offered as an explanation of bathmic evolution his hypothesis of *germinal selection*. But this is a pure assumption based upon Weismann's theory of the structure of the germ plasma, which is directly contradicted by observed facts (see *Heredity*).

The first reasonable hint of a cause for bathmic evolution has been furnished by Pearson in his theory of *reproductive, or genetic, selection*. From the study of four thousand three hundred and ninety families in the middle and upper classes, Pearson found that variations in fertility do not follow a normal symmetrical curve, but have a very skew distribution, small families being much more numerous than large ones. The result is that twenty-five per cent. of the parents produce fifty per cent. of the children. It is clear that on the average one pair of the smaller group of more fertile parents will have as much effect on the type of the next generation as three pairs of the larger less fertile group. Therefore, if fertility be inherited, and if there be a correlation between fertility and any other character, progressive change of type may take place by a purely bathmic process, unless checked by natural selection or other cause. As to the inheritance of fertility, Pearson found from a comparison of the sizes of the families of a thousand pairs of mothers and daughters, where the marriages had lasted fifteen years or more, that there was very good evidence of such inheritance. (He obtained a coefficient of heredity of .213 with a probable error of  $\pm .020$ .) Similar results were obtained by the study of one thousand pairs of paternal grandmothers and granddaughters. Here the coefficient of heredity ( $.112 \pm .021$ ) is about half as large as for mother and daughter, as would be expected by the law of ancestral heredity, and this is an example of the transmission of a female character through the male line with undiminished intensity. Thoroughbred horses also furnished evidence that fecundity is inherited between dam and daughter and also through the male line, fecundity being transmitted by a sire from his dam to his daughter. There is also evidence of correlation between fertility and other characters. In man, Pearson found that the more fertile women are slightly taller than the less fertile, and dark-eyed fathers and mothers are found to be more fertile than those with light eyes.

Poppies have radiating ridges on the upper part of the seed capsule, the stigmatic bands. In 4,443 capsules of Shirley poppies the range of variation was from 5 to 19 bands and the modal number was 13. Capsules with 12 to 13 bands were found to be very full of seed, while there were hardly any in capsules having very few or very many bands. Likewise in 3,212 seed capsules of *Nigella hispanica* the range of variation in the number of segments was from 2 to 20, with 8 for the modal number. Capsules with 8 segments were found to be very fertile, while those with 10, 11, and 12 segments contained hardly any seed, and those with 5 or less were practically sterile.

It is evident, then, that where the most fertile character coincides with the modal character, as in the case of the poppies and *Nigella*, this differential fertility, or genetic selection, will tend to preserve the stability of the race, and in order that differentiation of type may take place, this effect will have to be overcome. On the other hand, if the most fertile character differs from the modal character, as appears to be the case in the eye color of man, then there will be a progressive change, unless this is checked by preferential mating, natural selection, or some other cause. So differential fertility

is to be reckoned with as a factor in evolution. It is certainly in some cases a conservative factor, and it is possible that it may become a cause of progressive change of type. But whether bathmic evolution has ever taken place by this means without the aid of other factors is another of the unsolved problems.

**Inheritance of Acquired Characters.**—An "acquired" character is one which arises during the life of the individual as the result of functional activity or in response to an external stimulus. The term is an unfortunate one, for to many minds the word "acquired" conveys simply the impression of newness without regard to the source of the change. To meet this difficulty C. L. Morgan has proposed to use the term *modification* in place of acquired character, and to reserve the term *variation* for changes of purely congenital origin. Moreover, it is often difficult to distinguish between modifications and variations. For example, deafness may be due to congenital malformation of the ear, or it may be due to disease. In the first case it would be a variation, in the second it would be a modification. Now Fay in his study of the inheritance of deafness often found it difficult to decide in which class a given case should be placed.

The factors of organic evolution that we have examined so far have been the great factor, natural selection, and a number of others more or less aiding and accessory to it. We have seen that natural selection is itself conditioned by three other factors: (1) variation, (2) inheritance, and (3) the struggle for existence.

Natural selection is only indirectly concerned with the origin of variations. So long as variations are of the right kind and are capable of being transmitted, natural selection, with the aid of isolation, will protect and develop them. It is evident, then, that if the purposeful, adaptive modifications of the individual that arise as the result of its reactions to the stimulus of its environment may become hereditary, they will be a great aid to natural selection. For they will insure the presence of the right kind of variation to be selected when it is needed. Darwin thought that such acquired characters are inherited, and he regarded them as an important aid to natural selection. The neo-Lamarckians, on the other hand, have taken the view that the inheritance of acquired characters is much more than an aid to natural selection; that it is itself a prime factor of organic evolution.

Now comes the school of Wallace and Weismann, and says that the inheritance of acquired characters not only is not a prime factor in evolution, but it is not even an aid, as Darwin supposed, to natural selection. In fact, according to this school, acquired characters are not in any degree inherited. The question then is, Are acquired characters inherited, and if so, how far has this inheritance been a factor in the origin of species?

To discuss fully the subject of the inheritance of acquired characters as a factor of organic evolution would require much more space than we have at our command. But we may endeavor to present a few of the thoughts which seem to be of greatest importance in this connection.

In the first place, the neo-Lamarckian contention that the inheritance of acquired characters is the *prime factor* in evolution can be ruled out of court at once as manifestly untenable. There are a large number of structures in both plants and animals that can have developed only as the result of continued selection. Such are the cases of mimicry, both in form and color, warning colors, adaptations for cross fertilization in plants, and the like. But the most instructive examples, as pointed out by Brooks, are to be found in species having normally sterile individuals. In many species of polyps there are nutritive, offensive, or protective persons in each colony which never produce offspring; and among ants, bees, and termites, the most numerous and most active members of the community are sterile workers. These sterile individuals generally differ from the fertile males and females, presenting very beautiful modifications of both structures and instincts in adaptation to their very different functions and mode of life. Now as the worker has