CHAPTER III

HEREDITY AND VARIATION

"The organic world as a whole is a perpetual flux of changing types."—FRANCIS GALTON.

"Inheritance and variation are not two things, but two imperfect views of a single process."—W. K. BROOKS.

"Variation and inheritance are, at present, one fundamental mystery of the vital unit."—KARL PEARSON.

§ 1. *Persistence and Novelty*

CLOSE observers of the relation between successive generations in mankind, or among plants and animals, are at one in recording two distinct impressions,—on the one hand, of persistent hereditary resemblance, on the other hand, of variability. Oftenest we are first impressed by the remarkable homogeneity which obtains from generation to generation, but as we get to know the organisms better we become aware of individual traits standing out against the background of general similarity. Or it may be that, with the partiality of parents, our first impression is of the novelty and individuality of our children, and only later do we recognise in those, who seemed so original, a re-incarnation of our average selves. Oftener, perhaps, it will be discovered that the resemblance in habits of mind and body is purely *mimetic*, and that the idiosyncrasies which were really present, as buds at least, have been pruned off both for good and for ill by the hook of criticism, or driven into latency —like "sleeping-buds"—by mis-education or lack of appropriate stimulus.

Like Tends to Beget Like.—The hereditary relation is such that offspring are on the whole like their parents, but the degree of this likeness varies within wide limits. Indeed, the discrepancies are often very conspicuous, and we can understand how Prosper Lucas, one of the early students of inheritance (1847)—careful and scholarly according to his lights—imagined a metaphysical entity, which he called "*l'innéité*" and opposed to "*l'hérédité*," the former originating what is new, the latter conserving what is old. In modern phraseology, the occurrence of variations is a fact of life so general that we must replace the adage "Like begets like" with the more cautious statement "Like tends to beget like."

The popular adage "Like begets like" is often true as a general statement. Offspring are often so like their parents that even the scientific observer cannot tell one from the other. In other words, the species "breeds true." But the more intimate our acquaintance with organisms becomes, the more plainly do we detect individual peculiarities, and we have to change the adage to "Like tends to beget like." On the whole it is true that average parents have average offspring, that exceptional parents have exceptional offspring. Like tends to beget like. Yet it is well known that, for instance as regards stature, the tall do not always beget the tall, or the small the small, so that we have to broaden the most general "fact of inheritance" still further, and say that the average character attained by the individuals of one generation tends to be very nearly the same as the average character of the preceding generation. This is the broad fact of specific inertia.

A False Antithesis between Heredity and Variation.—Much obscurity of thought has been due to the false antithesis between heredity and variation. When we say that like tends to beget like, that offspring tend to resemble their parents and ancestors, we are stating a fact of life. But when we speak of an opposition between a force or principle of heredity, securing resemblance between offspring and their parents, and a tendency to variability which makes offspring different from their parents, we are indulging in verbiage. Heredity, as we have repeatedly said, is the relation of genetic continuity between successive generations, and it is such that while many characters seen in parents persist in their offspring, there is also in most cases a distinct individuality in these offspring. Heredity is a condition of evolution, a condition of inborn variations; it is just a name for the reproductive or genetic relation between parents and offspring. The inheritance which was expressed in the development of the parent may be almost identical with the inheritance which is expressed in the development of the offspring, but in most cases the inheritance does not persist in this intact way from generation to generation, and then we speak of variation. The contrast is not between heredity and variation, but between inertia and change, between continuity or persistence and novelty or mutation, between completeness of hereditary resemblance and incompleteness of hereditary resemblance.

As Prof. W. K. Brooks says (1906, p. 71): "Living beings do not exhibit unity and diversity, but unity in diversity. These are not two facts, but one. The fact is the individuality in kinship of living beings. Inheritance and variation are not two things, but two imperfect views of a single process."

§ 2. *The Tendency to Breed True*

Relative Stability of Specific Characters.—Belonging as we do to a race which seems to have varied very slowly within historic times, we have not far to seek for good examples of what is the biggest fact of inheritance—the stability of specific characters throughout a long series of generations. If we exclude monstrosities due to arrested development and the like, if we set aside the numerous malformations and deformations induced on the bodies of individuals by peculiarities of function and environment, the stability of the essential human characteristics for many millennia is obvious. This racial inertia, which holds in some measure at least for mental characteristics, is at once the hope and the despair of the social reformer.

If we pass from general specific characters to those of particular races, we read the same story. Not only do the salient characteristics of the skull persist within a narrow radius of variability, but the same is true of minor features: the oblique eyes of the Japanese, the oval face of the Esquimaux, the woolly hair of the Negro, the Austrian lip, and the Jewish nose.

Conservative Types of Organisation.—But the persistence of structural and mental characters as illustrated in mankind is but a tale of yesterday when compared with the persistence of type exhibited by many animals which have lived on apparently unchanged for many millions of years. Whatever may be true in regard to the soft parts, of which no record remains, there seem to be no differences in hard parts distinguishing the *Lingula* of to-day from those of the Silurian ages; and there are other instances of what are sometimes called "living fossils." The reasons for such remarkable persistence do not now concern us, but the fact that structural characters established millions of years ago are reproduced with exactness at the present moment does.

Persistent Peculiarities in Families.—Not less striking than the long persistence of specific and stock characters is the fact that offspring frequently reproduce the *individual* peculiarities—both normal and abnormal—of their parents or ancestors. A slight structural peculiarity, such as a lock of white hair or an extra digit, may persist for several generations. A slight functional peculiarity, such as left-handedness, has been recorded for at least four generations, and colour-blindness for five. There are endless illustrations of the fact that a pathological diathesis—rheumatic, gouty, neurotic, or the like—may persist and express itself similarly, even in spite of altered conditions of life, throughout many generations. And what is true of bodily characteristics is not less true of mental peculiarities: as to this, popular impressions and the careful investigations of Galton and others are in agreement.

§ 3. *Different Kinds of Organic Change*

It may conduce to clearness if we think over the different kinds of changes which occur in organisms.

1. **Metabolism.**—All living creatures are, as it were, whirlpools in the universal ocean of matter and energy. They are continually changing as they live. Streams of matter and energy pass in and out. Organisms are animate systems which transform matter and energy in a characteristic way which we call living. Their physical basis is continually undergoing destruction and reconstruction; it breaks down and is built up again, it wastes and is repaired, it runs down and is ever being wound up again—until the arrears of imperfect recuperation become so serious that the organism dies, or until some fatal accident occurs. The chemical and physical changes involved in living are summed up in the term metabolism, the two aspects of which—constructive and disruptive—are called anabolism and katabolism.

2. **Cyclic Changes.**—An equally familiar fact is that organisms pass through a series of changes. The fertilised egg undergoes cleavage, the resulting cells grow and differentiate, an embryo is formed, and gradually—often by circuitous paths—a miniature form of the adult creature is attained. Out of apparent simplicity an obvious complexity results. Growth still continues, often punctuated by resting periods, often rhythmic and

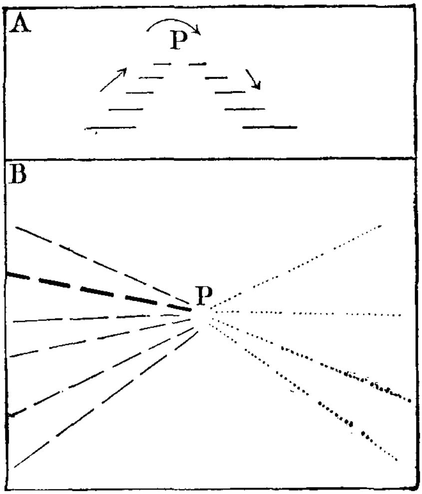

FIG. 17.—Diagram of protoplasmic changes—B in plan, A in elevation. The anabolic or constructive processes are represented to the left; the katabolic or destructive processes to the right. In B, one particular line of anabolic metabolism is supposed to be predominant.

expressible in complex curves, often interrupted by peculiar crises. Quickly or slowly the organism passes from youth through adolescence to maturity, to its limit of growth and its reproductive maturity. Quickly or slowly thereafter it sinks on a down-grade towards death. As the old naturalists said, from one period of vita minima the creature rises to a period of vita maxima, and sinks back again into a vita minima which dwindles to a vanishing point. It is characteristic of organisms to pass through a series of cyclic changes.

3. **Changes involved in Functioning.**—As contrasted with inanimate systems, organisms are characterised by their power of *effective response* to environmental stimuli. A living creature's responses tend towards self-preservation or species-preservation. Though they may fail, the reactions are primarily and fundamentally effective. And these functionings or effective responses necessarily involve changes in the system. They involve wear and tear, and leave more or less discernible results. Normally, however, the results, known as fatigue-effects and the like, are obliterated by nutrition, rest, and other forms of recuperation. In the study of an intricate structure, like a bee's brain, it is possible to arrange on an inclined plane the changes which are normally obliterated by a night's rest, the changes which require prolonged recuperation before they disappear, and the changes which cannot be recovered from—which accumulate until the bee dies a natural death.

4. **Temporary and Individual Adjustments.**—In addition to the inherent primary power of effective response, organisms have different degrees of plasticity. They can adjust their reactions to novel conditions. They can "try" first one mode of reaction and then another, finally persisting in that which is most effective. Even the unicellular Infusorians do this. How much of this plasticity is primary, or inherent in the very nature of living matter, how much of it is secondary and wrought out by Natural Selection in the course of ages, must remain in great measure a matter of uncertainty. Each case must be judged on its own merits. It is certain that many unicellular organisms are very plastic, and it seems reasonable to suppose that as differentiation increased, restrictions were placed on the primary plasticity, while a more specialised secondary plasticity was gained in many cases, where the organisms lived in environments liable to frequent vicissitudes. It is convenient to use the

term "accommodations" for the frequently occurring individual adjustments which many organisms are able to make to new conditions.

5. **Modifications.**—Besides being plastic, organisms are modifiable: that is to say, in the course of their individual life they are liable to be so impressed by changes in surrounding influences and by consequent changes in function that, as a direct result, modifications of bodily structure or habit are acquired. Modifiability is the capacity of registering the direct results of changed function or of changed environment. "Modifications" may be defined as structural changes in the body of an individual organism, directly induced by changes in function or in environment, which transcend the limit of organic elasticity and persist after the inducing conditions have ceased to operate. They are often inconveniently called "acquired characters." They are not proved to be transmissible as such or in any representative degree, but they are often adaptive and individually very valuable. They are distinguishable from temporary adjustments or accommodations on the one hand, and from inborn variations on the other.

6. **Inborn Variations.**—Finally, when we subtract from a total of "observed differences" between members of the same species all that can be described as accommodations and modifications, we find a large remainder which we must sharply define off as *variations*. We cannot causally relate them to peculiarities in habit or in surroundings; they are often distinct at birth or hinted at before birth; and they are rarely alike even among forms whose conditions of life seem absolutely uniform. They may be large or small in amount, fluctuations or freaks, progressive or retrogressive—that is a matter for further analysis—but they agree in having a germinal origin. They are endogenous, not exogenous; they are born, not made; and they are more or less transmissible, though they are not

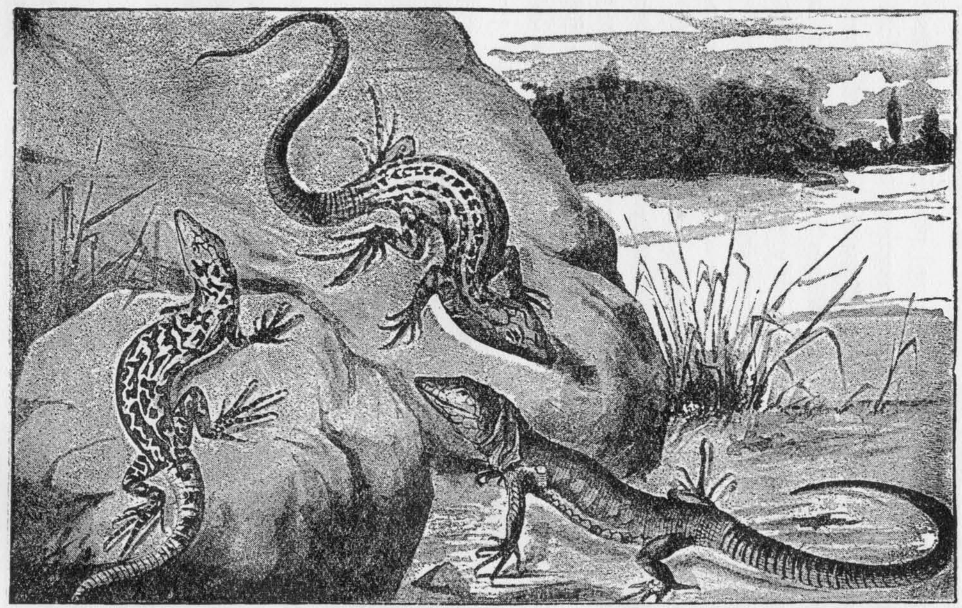

FIG. 18.—The wall-lizard (*Lacerta muralis*), three differently coloured and marked varieties of the same species. (Compiled from Eimer.)

always transmitted. They form—at least some of them form—the raw material of organic evolution.

§ 4. *Classification and Illustration of Variations.*

"Variation."—It is a common confession of naturalists that a label is a necessary evil. A collection without labels is a contradiction in terms, and yet the label is often a full-stop to investigation. This is true in regard to the concrete; it is more lamentably true in regard to the abstract. Thus the label "Variation" has been a great hindrance to progress.

As Mr. Bateson says (1905, p. 575): "The indiscriminate confounding of all divergences from type into one heterogeneous heap under the name 'Variation' effectually concealed those features of order which the phenomena severally present, creating an enduring obstacle to the progress of evolutionary science. Specific normality and distinctness being regarded as an accidental product of exigency, it was thought safe to treat departures from such normality as comparable differences: all were 'variations' alike."

All organic changes imply some incompleteness in the hereditary resemblance—a little more of one character, a little less of another, or the occurrence of some feature which deserves to be called distinctly "new." Both variations and modifications may cause this incompleteness in the hereditary resemblance; an apparently similar condition may result from two different processes of change. But the variation has a germinal origin, is blastogenic, is not directly dependent on the external conditions of life, is endogenous, and is transmissible; while the modification has a somatic origin, is the direct result of functional or environmental influence, is exogenous, and, so far as we know at present, is not as such transmissible.

Classification.—There are many different ways of classifying these variations which form the raw material of evolutionary change.

α. If we attend to the *nature of the change,* we may distinguish "*meristic*" variations—*e.g.* in the number and proportions of parts, from "*substantive*" variations of a qualitative sort—*e.g.* change in colour.

β. If we attend to the *direction of the change* in successive generations, we may distinguish "definite" variations, which occur along one line (like stages in normal development), from "indefinite" variations, which "fluctuate hither and thither with no uniformity in the course of generations."

Many evolutionists have maintained that there is good reason for believing in definite or determinate variation along particular lines, as if certain organisms had an inherent bias to change in certain parts and not in others, in certain directions and not in others, just as certain inorganic substances can crystallise in different forms but only within strict limits. It is possible to arrange a series of species A, B, C, D, E, F, in such a way that they suggest progressive definite variation along a particular line, and it seems not unlikely that this kind of evolution may sometimes occur. Moreover, along quite different lines of evolution we find evidence that the same kind of step has been taken independently, over and over again. This suggests that the possibilities of variations may be limited and defined by deep-rooted constitutional conditions or physiological alternatives. But the weakness of the argument lies in the almost insuperable difficulty of deciding whether the apparent definiteness is not the result of the primary action of selection which eliminates divergent variants at early stages—nipping idiosyncrasies in the bud—or which may have established a bias in previous generations. In conditions of rigid elimination the lines of variation will naturally tend to become more and more restricted.

γ. If we attend to *the amount of the change* from one generation to the next, we may distinguish minute fluctuations from sudden "sports" which reach a new position of organic equi-

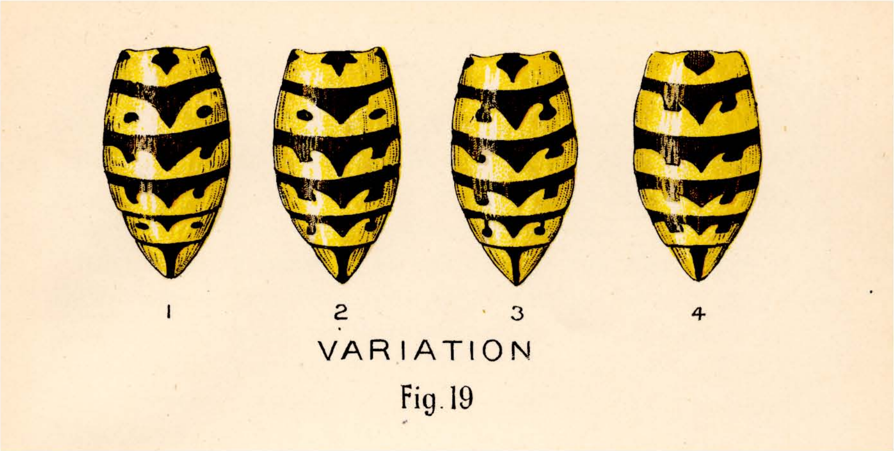

FIG. 19.—Some of the numerous variations in the pattern of the abdomen in the yellow-jacket Wasp. (After Kellogg and Bell).

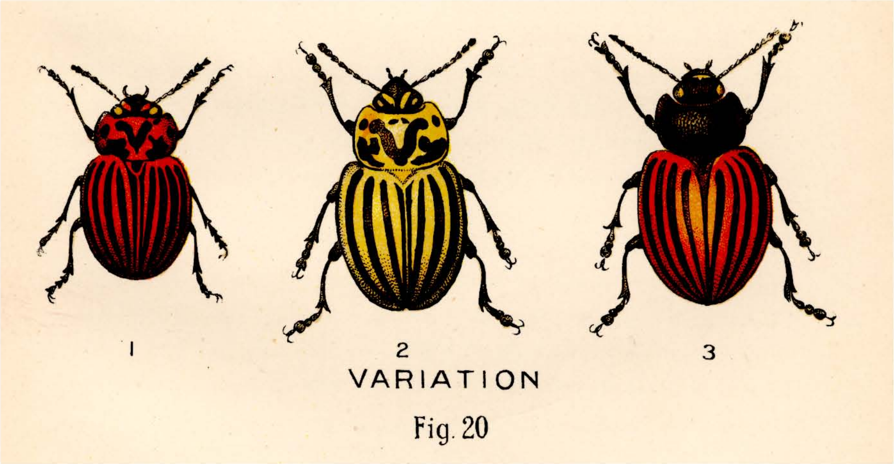

FIG. 20.—"Mutations" or rapidly developing large inheritable variations in *Leptinotarsa multitæniata*. The type of the species (2) and its extreme mutants *rubicunda* (1) and *melanothorax* (3). (After W. L. Tower

[*Facing p. 76.*

librium as if by a leap. We thus get the contrast between "continuous" variations small in amount, and "discontinuous" or "transilient" variations in which a step of considerable dimensions is taken with apparent suddenness.

Variations considered in relation to the Character of Antecedent Generations.—The term variation, used concretely to denote an organic peculiarity or idiosyncrasy, is obviously a relative term, implying some standard of comparison. It is a deviation from the parental type, a divergence from the mean of the stock.

In many cases, a variation may be described as simply an incompleteness in the inheritance or in the expression of the inheritance. The divergence from the norm is due to the suppression or inhibition of some character. This may be illustrated by a perfectly white (albino) baby, born to almost coal-black parents.* If such a form became the founder of an albino race, as in the case of rats and mice, we should be justified in concluding that the particular material organisation which eventually leads to the deposition of pigment in the body had somehow dropped out of the inheritance. If the albinism was in no respect transmitted to the next generation, we should be justified in concluding that the structural arrangements which lead on to pigmentation had simply been hindered from finding their normal expression in development.

A minus variation like albinism may be described as due to an incompleteness in the inheritance or in the expression of the inheritance, but there are other variations which must, so to speak, bear the plus sign, for they involve the augmentation or exaggeration of a character. Plus variations of this sort have

* "Its father and mother were horrified; their friends and relations, in fact all the villagers, were called to examine and criticise it. Why such surprise? Why such commotion? The answer is self-evident: the law of heredity had been broken."—R. W. Felkin. The vulgar mind is always impressed by size and quantity; big deviations strike the imagination, and the normal occurrence of small deviations is forgotten.

been taken advantage of in breeding sheep with long fleece, Japanese cocks with tails ten feet long, "wonder horses" with manes reaching the ground, and so on.

The recognition of minus and plus variations is simple and obvious, but it is not sufficient. For the offspring is sometimes so different from the parent that we cannot describe its peculiarity as an incompleteness in the expression of the normal inheritance, or as an exaggeration of parental or ancestral traits. It is sometimes a new pattern, a fresh departure, with what one might call organic originality. It is more than a discontinuous variation, for when the offspring of a horned race has no horns, or when the offspring is a giant, there is "discontinuity,"—an abrupt difference between parents and offspring. But what we are referring to here are those cases where the offspring seems to have passed suddenly into a new position of organic equilibrium, where it has not only individuality, but a distinctively novel individuality. It is convenient to call these variations by the special name *mutations*. They are novelties which arise brusquely.

§ 5. *Fluctuating Variations*

When we examine a number of individuals of the same species we usually find that they differ from one another in detail. Some of the observed differences may be modificational or due to differences of nurture, but it is often possible to abstract these from differences due to hereditary nature. Thus, when we collect a large number of specimens of the same age from the same place at the same time, we often find that no two are exactly alike. They have peculiarities of germinal origin—or, in other words, they show *individual or fluctuating variations*. Measurements in regard to any one character can be readily plotted out, and the result gives the curve of frequency.

The value of precise measurements of even trivial variations is great. The curves show at a glance the range of variability, the amount of a character that occurs with greatest frequency, and it is easy to deduce by various methods an index or measure of variability. Moreover the curves, especially if made year after year, may show the direction in which the species is moving, perhaps the way in which selection is working, perhaps even that the species is splitting up into two subspecies.

As we have said, these individual or fluctuating variations can usually be registered on the normal curve of frequency, such as is exhibited when results depend on a complexity of conditions. They are often called fortuitous or chance variations, but as this phrase always misleads the careless mind, it may be profitably dispensed with. Individual or fluctuating variations are often termed continuous, which means that any case differs but slightly from its parents, that the whole of them taken together form a continuous series, that one generation differs from another as the state of an embryo on one day differs from that of the next day.

Registration of Variations.—"The modern methods of statistics deal comprehensively with entire species, and with entire groups of influences, just as if they were single entities, and express the relations between them in an equally compendious manner. They commence by marshalling the values in order of magnitude from the smallest up to the largest, thereby converting a mob into an orderly array, which, like a regiment, thenceforth becomes a tactical unit. Those to whom these considerations are new, will grasp the results more easily by thinking of the array in its simplest, though not necessarily in its most convenient form for mathematical treatment. Let them conceive each value to be represented by an extremely slender rod of proportionate length, and the rods to be erected side by side, touching one another, upon a horizontal base.

The array of closely-packed rods will then form a plane area, bounded by straight lines at its sides and along its base, but by a flowing curve above, which takes note of *every one* of the values on which it is founded, however immense their multitude may be. The shape of the curve is characteristic of the particular group of values to which it refers, but all arrays have a family resemblance due to similarity of origin; they all drop steeply at one end, rise steeply at the other, and have a sloping back. An array that has been drilled into some such formation as this, is the tactical unit of the new statistics. Its outline is expressed by a general formula whose constants are adapted to each particular case, and being thus brought within the grip of mathematics, the internal relations of an array and their relations to those of any other array can be expressed in exact numerical forms." (*Biometrika*, vol. i., 1901, p. 7.)

Theory of Evolution by Selection of Fluctuating Variations.—It is certain that most offspring differ from their parents in many quantitative details. It is certain that when measurements are taken of a large number of individuals of the same species in reference to a particular character, the results, when plotted out, conform approximately to the normal curve of frequency. If measurements be taken in a subsequent generation there is a similar result, but the curve need not be precisely the same. The mode of the curve—*i.e.*, the most frequently occurring dimension of the measured character, may change from one generation to another. It is usually believed that one of the ways in which this change can be effected is by natural selection. But to think of new species arising by slow changes of this sort is in many ways difficult, apart altogether from the fact that definite demonstration of the operation of selection has been rarely attempted.

(1) Such a character as a Roman nose is certainly heritable, though it is not always inherited. But we cannot speak so

definitely in regard to small quantitative variations. A tall father does not necessarily have tall children. Where the characters in which the two parents differ are such as readily blend, regression towards the mean of the stock will occur.

(2) Even with very thorough isolation—segregation of like individuals—and very consistent selection, it is doubtful whether a new race could be evolved from the cumulative increase of small quantitative variations, *e.g.* in stature or colour of hair. It is doubtful whether any domestic races have so arisen. It is not in this way that dwarf-races and giant-races have been formed. They arise from sudden discontinuous variations or mutations, which are often peculiarly heritable, which are anything but liable to be swamped by inter-crossing, and which sometimes exhibit Mendelian inheritance.

(3) The result of the gradual accumulation of small quantitative variations may be very important in a long time, just as a small sum may become large from interest accumulated for centuries; *but it is difficult to believe that minute fluctuations* in quantity would always have sufficient selective value to ensure their persistence.

There are several reasons why selectionists have restricted themselves so much to continuous variations as the raw material of evolution. (1) Until lately we have known comparatively little in regard to discontinuous variations or mutations. (2) It was hastily concluded that these changes were not likely to be transmitted—a generalisation in part due to preoccupation with teratological non-viable freaks. (3) In many cases related species can be arranged in a gradual series with intermediate forms linking the extremes.

Now, there is no need to hamper the Evolution Theory by restricting selection to minute variations. We know that sports, mutations, or discontinuous variations are frequent, and that they are remarkably stable in their hereditary transmission.

We know also that many domestic races have, as a matter of fact, arisen by sudden mutation.

As to the series of related species which may be often arranged as if on an inclined plane, two points should be noted: (1) that it is likely enough that some kinds of species, *e.g.* vegetative forms like Alcyonarians and Corals, may have evolved by minute steps, and (2) that although species are often connected by intermediate links it does not follow that these links are stages in the evolution. They may have been formed *after* the species to which they are theoretically supposed to give rise. We should remember Galton's warning, "If all the variations of any machine that had ever been invented were selected and arranged in a museum, each would differ so little from its neighbours as to suggest the fallacious inference that the successive inventions of that machine had progressed by means of a very large number of hardly discernible steps." Many facts now lead us to conclude that the Proteus *leaps* as well as creeps.

§ 6. *Discontinuous Variations*

One of the steps of progress in Evolution-lore since Darwin's day is the recognition of the frequency and importance of discontinuous variations—*i.e.* of organic changes which arise abruptly and not by a gradual series of steps. If dwarfs arise suddenly in a tall race, and are not mere modifications, they illustrate discontinuous variation of a quantitative sort. A hornless calf, a tail-less kitten, a short-legged lamb, a thornless rose, illustrate discontinuous *quantitative* variations of a *negative* kind. Giants, "wonder-horses," long-tailed Japanese cocks, merino-fleeced sheep, spine-covered holly leaves illustrate discontinuous *quantitative* variations of a *positive* kind. Sometimes the novelty cannot be readily expressed in quantitative terms—an entirely new colour turns up, the variant is immune to certain diseases to which the stock is susceptible, leaves become fasciated, a tree becomes "weeping," a genius is born. It may be useful in such cases, where a new pattern of organisation or a new constitutional property turns up, to speak of a discontinuous *qualitative* variation.

Historical Note.—The idea that organic changes might come about by leaps and bounds is not novel, though the evidence substantiating it is quite modern.

Some of the older evolutionists, such as Etienne Geoffroy St. Hilaire, believed in saltatory evolution, and were far from agreeing with Lamarck that Nature is never brusque.

Darwin also recognised that big steps may be taken suddenly—*e.g.* in the origin of large-crested Polish fowls and short-legged Ancon sheep, but he thought that these discontinuous variations occurred rarely, and would be liable to be swamped by intercrossing. As every one knows, he relied mainly on the action of natural selection on the small, continuous, individual variations which are always forthcoming.

But the modern appreciation of the importance and frequency of discontinuous variations is mainly due to Bateson, who, in his *Materials for the Study of Variation* (1894), gave many instances of the sudden appearance of offspring which in some particular diverge widely and abruptly from their parents; and to De Vries, who has observed the occurrence of "mutations" in many plants, and has also followed them through generations, showing that they tend to breed true.

A Change of View.—Darwin and orthodox Darwinians relied in the main on the operation of selection on small individual variations—many of which are nothing more than quantitative fluctuations. If new adaptations and new discontinuous species arise in this way, the small variations must be heritable, the new character must be capable of cumulative increase by the persistent outcrop of similar variations generation after generation, the selection must be persistent and consistent, and a long time must be allowed.

Even when this theory is strengthened by subsidiary theories, *e.g.* as to the efficacy of isolation and germinal selection, it is more theoretically than practically convincing. It places such a heavy burden on the shoulders of Natural Selection that the idea of a leaping instead of a creeping Proteus has always been welcome.

But why are evolutionists now entertaining an idea—the importance of discontinuous variations—which Darwin considered and then rejected? The answer is that we now know of many instances of discontinuous variation in animals, and even more among plants, that we have some good evidence of these discontinuous variations or *mutations* "breeding true," and that we have in the theory of Mendelian inheritance a reason why a mutation which has once arrived should persist.

Some modern authorities go the length of saying that "mutations" form the sole raw material of evolution, and that "individual fluctuations" do not count at all. This seems an illustration of the common tendency to take up an extreme position in the enthusiasm of a new discovery. Because discontinuous variations are common and important it does not follow that continuous fluctuations are of no moment. Those "whose humour is nothing but mutation" confess that it is very difficult to distinguish between a small mutation and a large fluctuation. If the large fluctuation be heritable—which we may assume until it has been disproved—we confess that we do not see what is gained by trying to distinguish it from a small mutation.

The New View.—Dominated by the idea that "organisms are mere conglomerates of adaptative devices," and that these patents cannot but be the outcome of slow accumulation of minute fluctuations under the directive agency of selection, naturalists have paid little heed to the open secret that the living creature is inherently a Proteus suddenly and discontinuously passing from one guise to another by transilient variation.

Mr. Bateson (1905, p. 577) notes that Marchant in 1719 was the earliest to comment on the suggestiveness of sudden changes, such as he saw in plants of *Mercurialis* with laciniated and hair-like leaves which for a time established themselves in his garden. He suggested that species may arise in like manner. "Though the same conclusion has appeared inevitable to many, including authorities of very diverse experience, such as Huxley, Virchow, F. Galton, it has been strenuously resisted by the bulk of scientific opinion, especially in England.

"Upon whatever character the attention be fixed, whether size, number, form of the whole or of the parts, proportion, distribution of differentiation, sexual characters, fertility, precocity or lateness, colour, susceptibility to cold or to disease—in short, all the kinds of characters which we think of as best exemplifying specific difference, we are certain to find illustrations of the occurrence of departures from normality, presenting exactly the same definiteness elsewhere characteristic of normality itself. Again and again the circumstances of their occurrence render it impossible to suppose that these striking differences are the product of continued selection, or, indeed, that they represent the results of a gradual transformation of any kind. Whenever by any collocation of favouring circumstances such definite novelties possess a superior viability, supplanting their 'normal' relatives, it is obvious that new types will be created."

Heredity and Evolution.—Mr. Bateson has done good service in exposing to ridicule the prevalent misconception that domesticated races are "so many incarnations of the breeder's prophetic fancy." "Except in recombinations of pre-existing characters—now a comprehensible process—and in such intensifications and such finishing touches as involve variations which analogy makes probable, the part played by prophecy is small.

Variation leads ; the breeder follows. The breeder's method is to notice a desirable novelty, and to work up a stock of it, picking up other novelties in his course—for these genetic disturbances often spread—and we may rest assured the method of nature is not very different" (1905, p. 578).

This is obviously a very important change of view, though it is also in a way a return to what Darwin himself taught. "*Variation leads; the breeder follows.*" But more than that: Variation leads by leaps and bounds. As Mr. Bateson says, let the believer in the efficacy of selection operating on continuous fluctuations try to breed a white or a black rat from a pure strain of black-and-white rats by choosing for breeding the whitest or the blackest; or to raise a dwarf ("Cupid") sweet pea from a tall race by choosing the shortest. It will not work. Variation leads and selection follows.

Illustrations of Discontinuous Variation

Wonder Horses.—The so-called wonder-horse "Linus I." had a mane eighteen feet long and a tail twenty-one feet long. The parents and grandparents had unusually long hair. This seems a good illustration of a "sport" or discontinuous variation which not only persisted for several generations, but increased very rapidly.

Shirley Poppies.—The well-known Shirley Poppies arose from a single discontinuous variation, which may have occurred often before Mr. Wilks saved it from elimination and made it the ancestor of a prolific and distinctive stock.

Star Primrose.—The graceful star primrose (*Primula stellata*) arose as a sport from the conventional Chinese primrose, and was raised by Messrs. Sutton into a favourite stock. It had been thrown off before as a sporadic variety over and over again, but was "promptly extirpated because repugnant to mid-Victorian primness."

The Moth Amphidasys.—Some sixty years ago in the urban conditions of Manchester the black variety *doubledayaria* of the moth *Amphidasys betularia* found its chance, and soon practically superseded the type in its place of origin, extended over England, and appeared even in Belgium and Germany (Bateson, 1905, p. 577).

The Common Jelly Fish.—A good case of abundant discontinuity in variation is furnished by the common jelly-fish *Aurelia aurita*, whose sports have been studied by eight or more observers, from Ehrenberg (1835) onwards. Its parts are normally in multiples of 4 (4 equal areas in the radially symmetrical disc, 4 oral lips, 4 genital organs, 16 radial canals, 8 marginal sense-organs or tentaculocysts); but numerical sports are very common. These are sometimes irregular, *e.g.* when the radial symmetry of the disc is lost; but they are oftener quite symmetrical, *e.g.* when the animal has 2 genital organs, 2 oral lobes, 8 radial canals, and 2 marginal sense-organs.

In studying *Aurelia aurita* at Plymouth, Browne (1895) found that out of 1515 young forms (ephyræ) 21·4 per cent. had more or fewer than 8 marginal sense-organs, and that out of 383 adults 22·8 per cent. were similarly affected. The figures seem to show that the abnormal forms survive quite as well as the normal forms, yet there is no evidence that the sports were more numerous in 1895 than when Ehrenberg studied them sixty years before. In other words, although a plentiful crop of brusque variations is being continually supplied by this plastic form, there is no hint of the origin of a new race. (Bateson, 1894, p. 428.)

The Case of Pseudoclytia.—Although the numerous discontinuous variations of *Aurelia aurita* do not suggest that any new race is at present arising, it is possible to find an analogous case where it does seem that we have to do with a species newly arisen, or still in process of being established. A. G. Mayer found at the Tortugas, Florida, large numbers of a medusoid or swimming bell—*Pseudoclytia pentata*—a leptomedusan belonging to the family Eucopidæ. " It differs from all other Hydromedusæ in that it normally possesses 5 radial canals, 5 lips, and 5 gonads, all 72° apart, instead of 4 of these various organs 90° apart, as in other Eucopidæ." In the structure of its tentacles, otocysts, gonads, and manubrium, in the general shape of its bell, and the arrangement of its tentacles and otocysts, it is so closely similar to *Epenthesis folleata*, that it seems safe to conclude that the former has been derived from the latter or from some closely allied species. The two forms are somewhat different in colour and slightly different as to the position of the gonads, but the resemblance is exceedingly close, and no one can suppose that a medusoid with 5 radial canals is a primitive form. As there are pentamerous variants of *Epenthesis folleata* and tetramerous variants of *Pseudoclytia pentata*, we are not aware of any case which more cogently suggests the evolutionary interpretation. As Mayer says, " *P. pentata* may be called ' a new race ' in the sense that it is evidently derived from *Epenthesis*, and departs from the quadratic arrangement of organs, which is almost universal among Hydromedusæ. It is remarkably variable, and its great commonness attests to its successfulness in the struggle for existence" (Mayer, 1901, p. 20).

To obviate misunderstanding, it may be observed that by the term " newly arisen " which Mayer uses in reference to *Pseudoclytia pentata*, he means simply that " it has departed widely from the fundamental type of all other Hydromedusæ, and that it is apparently derived from a genus (*Epenthesis*) which is itself quite highly differentiated. It is, therefore, ' new ' in the sense that it cannot be a primitive form, although we have no means of determining how long a time it may have been in existence " (Mayer, 1901, p. 8).

While we cannot exactly demonstrate that *Pseudoclytia pentata* arose by discontinuous variation from *Epenthesis folleata*, or some closely allied form, the evidence in favour of that interpretation is exceedingly strong. It is interesting further to notice that "the newly-arisen species" is very successful as regards numbers, and that its variations have a strong family resemblance to those of its supposed ancestor, and are yet more abundant. In regard to its more abnormal variants, Mayer observes that they are handicapped by their loss of symmetry, for some are neither radial nor bilateral, and by a reduction of fertility even in cases where the number of gonads has been increased to six or seven.

The evidence from Medusæ and Medusoids is sufficient to show

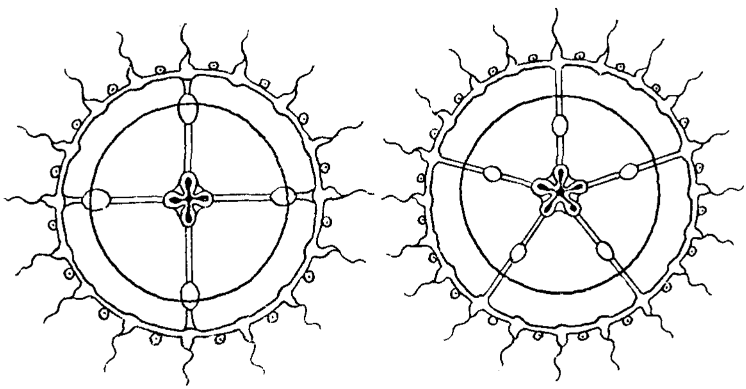

FIG. 21.—Mutation in Medusoids (after A. G. Mayer). The figure to the left is an oral view of *Epenthesis folleata.* The figure to the right is an oral view of *Pseudoclytia pentata.*

that discontinuous variations may occur in large numbers, that similar brusque changes may occur year after year, that there is sometimes a strong family resemblance in the variations of related forms. In some cases (*e.g.* in regard to *Aurelia aurita*) we are not in a position to say that anything has come of the abundant crop of discontinuous variations; in other cases (*e.g.* the very abnormal forms of *Pseudoclytia pentata*) the discontinuity has gone too far, as shown by the reduction of fertility and the entire loss of symmetry; while, thirdly, from the relationship of *Pseudoclytia pentata* to *Epenthesis folleata,* we are led to conclude that one species may arise from the discontinuous variation of another.

§ 7. *De Vries on Fluctuations and Mutations.*

Professor Hugo de Vries is one of the foremost of Darwin's intellectual heirs, with a rich endowment of his insight and patience. Long-continued and carefully controlled observations and experiments with generations of plants have led him to conclusions which have given the Evolution Theory a fresh start. His "Mutation Theory" is certainly one of the greatest advances since Darwin's day.

The General Idea.—The origin of species and varieties is an object for experimental inquiry. "Comparative studies have contributed all the evidence hitherto adduced for the support of the Darwinian theory of descent, and given us some general ideas about the main lines of the pedigree of the vegetable kingdom, but the way in which one species originates from another has not been adequately explained. *The current belief assumes that species are slowly changed into new types. In contradiction to this conception the theory of mutation assumes that new species and varieties are produced from existing forms by sudden leaps. The parent-type itself remains unchanged throughout this process, and may repeatedly give birth to new forms. These may arise simultaneously and in groups, or separately at more or less widely distant periods.* . . . . My work claims to be in full accord with the principles laid down by Darwin, and to give a thorough and sharp analysis of some of the ideas of variability, inheritance, selection, and mutation, which were necessarily vague at his time" (From preface to *Species and Varieties, their Origin by Mutation*" Chicago and London, 1905).

A Theoretical Implication.—De Vries's Mutation Theory involves the theoretical conception that "the characters of the organism are made up of elements that are sharply separated from each other. These elements can be combined in groups, and in related species the same combinations of elements recur. Transitional forms like those that are so common in the external features of animals and plants do not exist between the elements themselves, any more than they do between the elements of the chemist."

It is interesting to notice that whether we consider Weismann's theory of the determinants composing the germ-plasm, or the Mendelian theory of the segregation of characters in the germ-cells, or De Vries's Mutation Theory, we are led to the theoretical conception of elementary units. And again, we find the late Professor Weldon referring to Galton's Law in the following terms: "The Galtonian theory postulated the presence of 'elements' in the germ-cells of one generation, which are of two kinds—viz. active or dominant elements and groups of elements which determine the heritable characters of the progeny or second generation, and latent or recessive elements which passed through the bodies of one or more generations without appearing to affect them" (*Lancet*, March 25th, 1905, p. 810).

The Case of the Evening Primrose.—In 1886, De Vries began hunting about around Amsterdam for a plant which would show hints of being in what we may call a changeful mood. He tried over a hundred species, bringing them under cultivation, but almost all were disappointingly conservative. It seemed as if most of the species around Amsterdam were in a non-mutable state. It is possible, as Weismann suggested in one of his first evolutionary essays (1872), that in the life of species periods of constancy alternate with periods of changefulness. The human historian has often made a similar remark.

In the course of his wanderings around Amsterdam, De Vries came across a deserted potato-field at Hilversum—a field of treasure for him. For there he found his long-looked-for mutable plant, an evening primrose (*Œnothera lamarckiana*). Like its nearest relatives, *Œnothera biennis* and *Œnothera muricata*, which it excels in size and beauty of flowers, it probably came from America, where it is a native. It had probably "escaped" at Hilversum about 1875, and in the following ten years it had spread in hundreds over the field. It had been extremely prolific in its freedom, but that was not its chief interest.

Its chief interest was its changefulness. It had, so to speak, frolicked in its freedom. Almost all its organs were varying—as if swayed by a restless tide of life. It showed minute fluctuations from generation to generation ; it showed extraordinary freaks like fasciation and pitcher-forming ; it showed hesitancy as to how long it meant to live, for while the majority were biennial, many were annual, and a few were triennial ; best of all, it showed what can hardly be otherwise described than as new species in the making.

It is possible that the prolific multiplication in a new environment may have had something to do with the awakening of the impulsive mutability.

In 1887, a year after his discovery of the potato-field, De Vries found two well-defined new forms—a short-styled *O. brevistylis* and a beautiful smooth-leaved *O. lævifolia*—distinguishable from the parent *O. lamarckiana* in many details. He hailed these as two new "elementary species," * and he applied one of the crucial tests of specific or subspecific rank: Did they breed true? He found that this was so ; from their self-fertilised seeds similar forms arose. Neither of the two new forms was represented in the herbaria at Leyden, Paris, or Kew ; neither had been described in the literature of Onagraceæ. They seemed to be distinctively new. It is interesting to note that in 1887 there were few examples of these two new elementary species, and that each occurred on a single plot in the field. The impression conveyed was that each had arisen—by a sudden mutation—from the seed of an individual parent.

The next chapter in the famous investigation began with a transference of samples of the new forms and the parent

* By an "elementary species" is meant simply a group of individuals which agree with one another and differ from other groups in a certain number of characters, normally constant through successive generations.

stock—partly as plants and partly as seeds—from the potato-field at Hilversum to the botanic garden at Amsterdam.

The three stocks gave rise under cultivation to many thousands of individuals, which bred true along certain lines, and yet gave rise to other new forms. In short, De Vries had found a plant in process of evolution. The predisposition to mutability—which remains a mystery—was present, De Vries gave it scope, and like the primeval gardener he had the pleasure of giving names to a crop of new creations which emerged before him. From each of his three samples there arose several distinctive groups—which if they had been found in nature would have been reckoned as distinct species of evening primrose. But the most interesting feature was the apparent abruptness in the origin of the new forms. They seemed to arise by leaps and bounds, by organic jerks ; they illustrated what De Vries has called " Mutation."

Besides the smooth-leaved *O. lævifolia* and the short-styled *O. brevistylis*, both of which appeared in the potato-field, the cultivation of *O. lamarckiana* resulted in the emergence of seven constant elementary species—*O. gigas* (rare), *O. rubrinervis*, *O. oblongata*, *O. albida*, *O. leptocarpa*, *O. lata*, and a dwarf *O. nanella*. Besides these there were a few inconstant variants and a few which were sterile.

One form, *O. scintillans*, that only appeared eight times, was not constant like the others. When self-fertilised it produced *O. oblongata*, *O. lamarckiana*, and others like itself.

It is interesting to notice that some of the forms—*e.g. O. oblongata*,—were produced over and over again ; that five of the new forms appeared afterwards in the field or from seeds collected in the field, which shows that the cause of their origin was not to be found in the cultivation.

As De Vries says, the new elementary species arise suddenly without transitional links ; for the most part they are quite constant ; within the limits of their essential constancy they exhibit similar minor fluctuations ; they are usually represented by numerous individuals within the same period of time ; the observed changes affect many organs and parts, and in no definite direction; and the mutability seems to be periodic, not continuous.

If cases like that of *O. lamarckiana* are indicative of what often occurs and has occurred in nature, then our view of the evolution-process must be in several respects modified.

It will be necessary to distinguish more sharply between fluctuating variations and discontinuous mutations. If a new elementary species may arise as it were ready-made, "at a single advance," it is not necessary to hold to the formula that species have arisen by the gradual accumulation (under selection) of minute individual variations. As mutations occur in large numbers and occur repeatedly and are very constant, the familiar difficulties in regard to the swamping of novelties, the inappreciable value of incipient stages, the apparent non-utilitarian character of some specific differences, and so on, will be greatly lessened. The reader may be referred to Prof. T. H. Morgan's *Evolution and Adaptation* (1903) for a valuable discussion of the advantages of the Mutation Theory.

De Vries's Analysis of Variation.—In order to appreciate more thoroughly the importance of the changes which De Vries has necessitated in our evolutionary conceptions, we must briefly refer to his analysis of the distinct phenomena which have been too often unfortunately slumped under the title "Variations."

"Elementary Species."—In many groups of organisms which are usually called Linnæan species, there are several or numerous "subspecies," or "varieties." They remain more or less constant in their characters from generation to generation, they breed true in artificial conditions, they are not local races with similar modifications; De Vries calls them "elementary species." Thus there are about two hundred "elementary species" of the common Crucifer, *Draba verna*, and a few "elementary species" of the common European heartsease (*Viola tricolor*), and so on.

"The systematic species," De Vries says, "are the practical units of the systematists and florists, and all friends of wild nature should do their utmost to preserve them as Linnæus has proposed them. These units, however, are not really existing entities; they have as little claim to be regarded as such as the genera and families have. The real units are the elementary species; their limits often apparently overlap, and can only in rare cases be determined on the sole ground of field-observations. Pedigree-culture is the method required, and any form which remains constant and distinct from its allies in the garden is to be considered as an elementary species" (1905, p. 12).

Elementary species are considered to have originated from their parent form in a progressive way; they have succeeded in attaining something quite new for themselves.

Retrograde Varieties.—De Vries applies this term to those numerous forms which have thrown off some peculiarity characteristic of their ancestors. Like elementary species they may arise suddenly, but while "progressive steps are the marks of elementary species, retrograde varieties are distinguished by apparent losses." Retrograde varieties usually differ from their parent species by a single sharp character only,—they have lost pigment, or hairs, or spines, and so on; while elementary species are distinguished from their nearest allies in almost all organs. Moreover, the same kind of retrograde variety occurs repeatedly in different series of species, hence the long lists of unrelated varieties called by the same varietal title—*e.g.* *alba*, *inermis*, *canescens*, or *glabra*.

"Varieties differ from elementary species in that they do not possess anything really new. They originate for the greater part in a negative way, by the apparent loss of some quality, and rarely in a positive manner by acquiring a character already seen in allied species" (1905, p. 152).

Ever-sporting Varieties.—De Vries uses this term to describe cases like the striped larkspur, which for centuries has gone on producing unstriped as well as striped flowers. "Its changes are limited to a rather narrow circle, and this circle is as constant as the peculiarities of any other constant species or variety. But within this circle it is always changing, from small stripes to broad streaks, and from them to pure colours. Here the variability is a thing of absolute constancy, while the constancy consists in eternal changes!" Plants with variegated leaves, with double flowers, with fasciated branches, with peloric flowers, and so on, often illustrate the "ever-sporting" tendency. The common snapdragon (*Antirrhinum majus*) is a very good case,—the striped variety, for instance, cannot be fixed. There is some inherent instability in the combination of unit-characters in these ever-sporting varieties.

Fluctuations.—De Vries applies this term to the continually occurring individual variations. "It is normal for organisms to fluctuate to and fro, oscillating around an average type. Fluctuations are linear, amplifying or lessening the existing qualities, but not really changing their nature. They are not observed to produce anything quite new; they always oscillate around an average, and if removed from this for a time, they show a tendency to return to it." They are inadequate ever to make a single step along the great lines of evolution, whether progressively or retrogressively. They do not form the raw material of evolution, as has often been supposed. But, we submit, it is difficult with our present knowledge to discriminate between a fairly large fluctuation and a small mutation.

Mutations.—"In contrast to the ever-recurring variability, never absent in any large group of individuals, and determining the differences which are always to be seen between parents and their children, or between the children themselves, we have to rank the so-called sports or single varieties, not rarely denominated spontaneous variations, for which I propose to use the term 'mutations.' They are of very rare occurrence, and are to be considered as sudden and definite steps" (1905, pp. 190–1).

"De Vries recalls Galton's apt comparison between variability and a polyhedron which can roll from one face to another. When it comes to rest on any particular face, it is in stable equilibrium. Small vibrations or disturbances may make it oscillate, but it returns always to the same face. These oscillations are like the fluctuating variations. A greater disturbance may cause the polyhedron to roll over on to a new face, where it comes to rest again, only showing the ever-present fluctuations around its new centre. The new position corresponds to a mutation" (T. H. Morgan, 1903, p. 289).

According to De Vries, mutations have furnished the material for the process of evolution.

The Oldest Known Mutation.—A few years before the close of the sixteenth century (1590), Sprenger, an apothecary of Heidelberg, found in his garden a peculiar form of *Chelidonium majus* or greater celandine. It was marked by having its leaves cut into narrow lobes with almost linear tips, and by having the petals also cut up. This sharply defined new form suddenly appeared among the plants of *Chelidonium majus* which the apothecary had cultivated for many years. It was recognised by botanists as something quite new, and eventually it got the name *Chelidonium laciniatum*; it was not to be found wild, or anywhere except in the Heidelberg garden. But from the first this new cut-leaved celandine proved constant from seed. It has been naturalised in England and other countries, and is sometimes now found as an "escape." Its origin by mutation seems as certain as its constancy. It is further of interest to note that in crosses with *C. majus* it follows the law of Mendel.

Summary.—De Vries has done great service in analysing the complex concept of variation; in sharply contrasting individual fluctuations and mutations; in defining "elementary species," "retrograde varieties," and "ever-sporting varieties";

in observing the actual origin by mutation of stable new varieties or subspecies of *Œnothera lamarckiana* and some other plants; in showing by historical research combined with experiment that many stable stocks of cultivated plants have arisen by mutation; and by corroborating throughout the fundamental idea that "the characters of organisms are composed of units sharply distinguished from one another."

The contrast between fluctuations and mutations is so important that we may state it once more. (1) Fluctuations are continually occurring generation after generation: mutations are rare and occur intermittently. (2) Fluctuations give rise to a series of minute differences which may be arranged on a frequency curve, according to the laws of chance: mutations may be large or small, and their occurrences do not illustrate any ascertained law of frequency. (3) Fluctuations do not lead to a permanent change in the mean of the species unless there be very rigorous selection, and even then, if the selection be slackened, there is regression to the old mean: mutations lead *per saltum* to a new specific position, and there is no regression to the old mean. (4) Fluctuations do not yield anything really new, they imply a little more or a little less of characters already present: mutations are novelties, they imply some new pattern, some new position of organic equilibrium. According to De Vries's theory, no new species can be established without mutation. "When a mutation has occurred a new species is already in existence, and will remain in existence, unless all the progeny of the mutation are destroyed." . . . . The phrase "survival of the fittest," as describing a process of evolution, ought to be replaced by "survival of the fittest species." According to De Vries, species originate by mutation instead of by the continuous selection of fluctuations. "Natural Selection may explain the survival of the fittest, but it cannot explain the arrival of the fittest."

In regard to these far-reaching conclusions it should be noted

Fig. 22 —-Mutations of Hart's Tongue Fern *(Scolopendrium vulgare)* After Lowe.

1, Typical; 2, variety sagittato-cristatum; 3, reniforme; 4, cristatum; 5, contractum; 6, stansfieldii.

Facing p. 98.

that while De Vries has given much convincing evidence in regard to plants, we have as yet very slight evidence of the origin of species of animals by mutation. We know of many discontinuous variations among animals, but the subsequent history of these is not known except in a few cases. It must be remembered that, morphologically regarded, the whole vegetable kingdom does not correspond to more than the first three or four phyla in the animal kingdom—to the Protozoa, Porifera, and Cœlentera, where, as in plants, the contrast between germ-plasm and somatoplasm has not been accentuated, as it is in higher animals. It is quite conceivable that a mode of evolution common among plants may be rare among animals. It is difficult at present to apply the mutation concept with security to the animal kingdom.

The idea of mutation is very welcome because it lessens the burden which it has been found theoretically necessary to lay on the shoulders of the selection hypothesis, and because it fits in well with the *a priori* convictions which some naturalists have as to the autonomy of the organism, that it is as much a self-changing insurgent Proteus as a pawn in a game which the Environment plays. But because it is so welcome, it is to be entertained the more cautiously. An authority on domesticated animals, Prof. Keller of Zürich, finds but little evidence of it in the history of the well-known stocks.

It seems to us that in emphasising the importance of mutations De Vries has swung to the extreme of greatly depreciating the importance of fluctuations. Until we know more about animal mutations, it does not seem to us legitimate to deny that fluctuations may form, as Darwin believed, an important part of the raw material on which selection operates.

We cannot but regard with suspicion the distinction between large fluctuations and small mutations. It seems to us a verbal distinction.

Finally, it must be remembered that, as De Vries frankly points out, we are ignorant in regard to the conditions in which mutations occur. The Mutation Theory does not as yet give us a theory of mutations.

§ 8. *Causes of Variation.*

In regard to the causes of variation it is too soon to speak, except in tentative whispers. What Darwin said must still be said: " Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part has varied."

Variability.—The difficulty which every naturalist has felt in trying to define the concepts of variability and variation is due to the fact that living creatures are individualities—in some degree, personalities. In the ocean of matter and energy organisms are, as it were, whirlpools, each one with a particular character of its own. They are animate systems, each with a unity or individuality which we cannot fully interpret. They have the power—again an ultimate prerogative—of giving rise to other whirlpools, to other animate systems, which tend to be like themselves. But because each organism is a very complex whirlpool in a very complex environment, and because a living individuality cannot reproduce others without subtle molecular manœuvres which we know only in a far-off sort of way, one individuality is very unlikely to reproduce an absolute facsimile of itself. It is of the very essence of a living thing to change, and an individuality cannot be halved. From this point of view, variation is a primarily normal occurrence, and breeding true has secondarily come about as the result of restriction. In short, variability is a primeval character of organisms. We cannot explain variability; it is a datum in the world of life. We may, however, try to show in certain cases how it operates and what conditions help or hinder it.

The unending problem of life is to establish some sort of *modus* *vivendi* between an extremely complex and changeful animate system and the extremely complex and changeful environment in which it lives and moves and has its being. In all viable organisms this equilibration has been established, and it is plain that those organisms which could secure an entailment of this equilibration would be the organisms to survive. The producers of survivable descendants survive in them—an obvious economy of successful experiment, if such a point of view can be entertained.

We have seen that during the early stages of development there is often a visible segregation of a lineage of germ-cells which do not share in body-making, but continue like the fertilised ovum. This distinction between somatic cells which undergo differentiation and germ-cells which retain the heritable qualities intact is obviously an advantageous method of entailing on successive generations that valuable asset which we have called organic equilibration. It also economises and facilitates the process of reproduction.

But in spite of this almost universal device, the general tendency of which is to secure persistence, continuity, and complete hereditary resemblance, there is abundant opportunity left for the assertion of that variability which we believe to be a primary quality of vital units. Thus an inquiry into the causes of variation seems to us to be in the main an inquiry into the opportunities for the reassertion of a pristine tendency which the continuity of the germ-plasm has to some extent restricted. The stream of life passing through a continuous lineage of germ-cells is, so to speak, hemmed in, but it continually tends to deviate from this course, and there are not a few opportunities—some normally recurrent, some more accidental—which allow of this or even prompt it. In some cases, as we have said, it is impossible to distinguish offspring from parent, or brother from brother, or cousin from cousin. On what does this completeness of hereditary resemblance (*i.e.* the absence of variation) depend ?

It means, in the case of unicellular organisms, that the separated parts are identical in substance and carry on the complete organisation of the parent cell in absolute integrity. In the case of multicellular organisms it depends on the same thing. The cell which in the embryo begins the germ-cell lineage may be identical with the fertilised ovum, and the complete heritage may be continued intact through successive cell-divisions until the next generation is started, and the process begins anew. The completeness of hereditary resemblances depends, in Bateson's phrase, on "that qualitative symmetry characteristic of all non-differentiating cell-divisions."

It seems, therefore, useful to say that variation is "the expression of a qualitative asymmetry beginning in gametogenesis. Variation is a novel cell-division." But to tell what specific cause induces this novelty is still beyond our power. Yet we can point to certain conditions which may induce novelty or qualitative asymmetry in gametogenesis. Thus, there is the complex changeful environment of the developing germ-cells, there is the possible struggle of analogous hereditary units or determinants for sustenance, there is the complex process of reduction which occurs during the maturation of the germ-cells, and there are the chances of new combinations and permutations in fertilisation.

Results of Amphimixis.—That amphimixis is one of the provocatives of variations is strongly suggested by what results when two breeds are interbred. As Prof. Cossar Ewart says *: "Domestic animals reproduce themselves with great uniformity if kept apart; but the moment one mixed up two different races, strains, or breeds, one did something that was difficult to put in words, but the result was what has been best described as an 'epidemic' of variations."

* Discussion on Heredity in Disease, *Scottish Med. and Surg. Journal*, vi. 1900, p. 308.

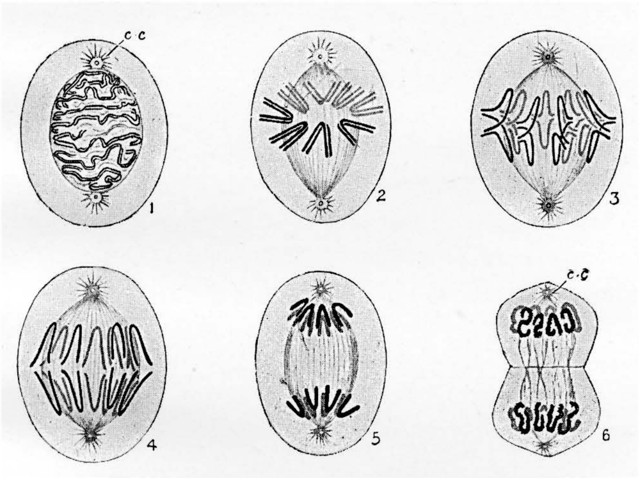

FIG. 23.—Karyokinesis. (After Flemming.)

1, Coil stage of nucleus; *cc* centrosome; 2, Division of chromatin into U-shaped loops, and longitudinal splitting of these (astroid stage); 3, 4, Recession of chromosomes from the equator of the cell (diastroid); 5, nuclear spindle with chromosomes at each pole, and achromatin threads between; 6, Division of the cell completed.

[*Facing p.* 102.

On the other hand, Hatschek and others have pointed out that amphimixis acts as a check on variability, obviating heterogeneous idiosyncrasies. This was suggested even by Lamarck: "In reproductive unions the crossings between the individuals which have different qualities or forms are necessarily opposed to the continuous propagation of these qualities and these forms." Similarly Darwin said: "When species are rendered highly variable by changed conditions of life, the free intercrossing of the varying individuals tends to keep each form fitted for its proper place in nature."

Combinations of Chromosomes.—Prof. H. E. Ziegler has given much attention to the number of possible combinations of parental chromosomes in the offspring, supposing the distribution to be fortuitous. If the normal number of chromosomes in a species is n, the number of tetrad groups is $\frac{n}{2}$, the number of possible combinations in the mature germ-cells is $\frac{n}{2} + 1$, and the number of possible combinations in the fertilised egg-cell is $\left(\frac{n}{2} + 1\right)^2 = \frac{n^2}{4} + n + 1$. If the normal number of chromosomes be 8 (as in the fluke often found parasitic in frogs, *Polystomum integerrimum*), the number of tetrad groups is 4, the number of possible combinations in the mature germ-cells is 9, and the number of theoretically different offspring is 25, *i.e.* on the assumption that the chromosomes are heterogeneous. But according to the laws of chance certain combinations are much more frequent than others; the larger the number of tetrad groups the more frequent is the occurrence of an approximately equal number of paternal and maternal chromosomes in the germ-cell.

Sutton puts the matter as follows. An individual receives from his father 4 chromosomes, A, B, C, D, and from his mother (an equal number) a, b, c, d. The immature germ-cell has A, B, C, D; a, b, c, d. These group themselves in four tetrads, each composed of two double chromosomes, two maternal and two paternal, Aa, Bb, Cc, Dd. The mature germ-cell receives one chromosome from each tetrad, and there are 16 possible combinations—viz. a, B, C, D; A, b, C, D; A, B, c, D; A, B, C, d; a, b, C, D; a, B, c, D; a, B, C, d; a, b, c, d; and eight others which may be got by replacing small letters by capital letters and *vice versâ*. The number of possibly different offspring would be 16^2.

Sutton gives the following table, which is of some interest as suggesting the possibilities of variation.

Normal number of chromosomes	Number of Tetrad-groups	Number of combinations in the mature germ-cells	Number of possibilities in the offspring
8	4	16	256
12	6	64	4,096
16	8	256	65,536
24	12	4096	16,777,216

Summary.—In certain moods biologists are accustomed to say that they do not know anything in regard to the causes of variation. They imply that it is of the essence of living creatures to vary, that variability is a primary property of organisms. The sequence of generations is a life stream, changing as it flows.

In other moods, however, biologists often point out how natural it is that organisms should vary. When the body of the parent is a-making, a lineage of germ-cells is started and the unspecialised descendants of these develop into offspring, which are on the whole like the parent because they are made of the same stuff. "True" twins developed from one ovum are usually almost facsimiles of one another. Why should not the offspring be a facsimile of the parent? Sometimes, *to our eyes*, it is quite confusable with the parent, but this is not common. Why not?

1. It is common to point out that the germ-cell which is liberated to become an offspring is not likely to be identical with the germ-cell which developed into the parent. It has been sojourning in the parent's body, exposed to a variable food stream and often to a variable complex environment, partly somatic and partly external. Is it likely to be exactly the same as the original germ-cell from which it is descended by continuous cell-division?

2. It is also to be remembered that if the heritable qualities have their vehicle in the chromosomes, as seems practically certain, then there is during the maturation of the germ-cells a

reduction of the chromosomes to one half their original number. This offers an opportunity for variation.

3. It is likely that fertilisation or amphimixis—the intimate and orderly union of two sets of hereditary contributions which have often had very different histories—will promote variation. It is difficult to believe that it does not bring about new permutations and combinations.

4. It is possible that variations may also arise in a less conceivable fashion—"bathmically," as the phrase goes—for unknown internal reasons. It is not absurd to suppose that the germ-plasm grows from generation to generation, and, in growing, changes—because it is its nature so to do.

Apart from variation of internal origin and positive modification of external origin, we must remember that the offspring may differ from its parents through non-expression of certain items of its inheritance, the non-expression being due to the absence of the appropriate liberating stimulus. This kind of deviation may of course be obliterated next generation, when the full environment allows the latent character to re-express itself.