PART III—VARIATION.

THE STUDY OF VARIATION.* BY C. H. EIGENMANN.

VARIATION AND ITS IMPORTANCE. No two individuals are exactly alike. The differences of whatever sort, whether in structure or habit, between the individuals of a species, whether these individuals are related to each other as parent and child, or belong to the same brood, are termed variation.

The whole basis of the Darwinian idea of evolution is this individual variation. At present we have two estimates of the importance of individual variation.

I. The individual variations are of the utmost importance, and all species are the result of natural selection working on the varying individuals of any species.

II. Individual "variation offers us little hope of learning the real facts of evolution," "species are not the result of the selection of a few favorable variations out of a large number of haphazard changes," but to "the orderly advance (of the mean specific form) towards the final goal, deviating very little from the direct line."†

We subscribe to neither of these views, wishing to view the facts as they are presented by the conditions of the environment at Turkey Lake and the lakes in the neighborhood, in a perfectly impartial way.

The causes of variation are still unknown, though several explanations have been attempted. This is not surprising since the variations in no species are sufficiently known to formulate any satisfactory explanation, in fact little has been attempted but to determine the extent of variation in comparatively few cases where the variation is great, resulting in the naming of new varieties and in the recording of abnormalities. The statistical method of studying variation is of the most recent date, but much promises to be done with this method.

DISTRIBUTION OF VARIATIONS. Variations are to be found at all times and at all places where organisms exist. They are found under conditions where the environment is in a state of stability. The conditions under which the greatest variability is found (in fishes) are:

1. Wide distribution. A large territory is, usually, though not necessarily, inhabited by more or less stable varieties.

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*Contributions from the Zoölogical Laboratory of the Indiana University, No. 17.

†This wording is from Scott, but since the paragraphs are selected from isolated parts of his paper, I do not wish to convey the idea that they state his views as he would like to have them stated. The paragraphs state an extreme view.

2. Great physical and climatic differences, even in comparatively narrow limits. No more striking illustration can be imagined than is offered by the streams of the Pacific slope of North America, which are inhabited by extraordinary variable species, without stable varieties

3. Amphimyxis has been suggested by Ayres as a condition favoring the display of great variation.

These are simply statements under which variation seems to find its optimum condition and do not approach any explanation of its causes.

Classifications of Variations.—Students of variation have found it advantageous to analyze the phenomena, and the result of this analysis has given us the following classifications:

Continuous variation, including all gradual modifications and transitions.

Discontinuous variation ; any sudden and wide modifications or saltations.

Using other features as the basis of classification, we have :

Meristic variations dealing with the change in the number of successive parts.

Substantative dealing with the chemical modifications of parts.

Another classification gives us :

Indeterminate, or fortuitous and aimless variation. This is largely individual and pertains to series of variations either geographically or geologically.

Determinate and adaptive, leading to definite end.

The most essential and at the same time the most difficult to define is the distinction between—

Ontogenetic variation including all those deviations appearing at any time, from any cause, during the life cycle of an individual;

Phylogenetic variations change from the specific characters appearing at some time in the life cycle of an individual, or better still, a large number of individuals, reappearing in the next generation, finally becoming hereditarily fixed.

I have in the following directions omitted the use of the terms ontogenetic and phylogenetic. Recently (Osborn, 1894), the distinction between ontogenetic and phylogenetic variation in the study of evolution has been strenuously insisted upon as the only possible way of determining the value of any given variation in the process of evolution. However, it is certainly impossible in many cases to determine whether a given variation is ontogenetic or phylogenetic as defined by Osborn. To give a concrete case. The ancon sheep of evolutionary classics was born with short legs. Were they ontogenetic or phylogenetic? Subsequent events proved that they were phylogenetic, but certainly the short legs in themselves enabled no one to make the distinction; the hereditary transmission decided the matter. Sports, therefore, of which the ancon sheep was certainly one, may be phylogenetic. Scott, however, has recently shown, Am. J. Science, 369, 1894, that many if not most saltatory variations are of an entirely different nature from the variations that in the past have given rise to phylogenetic series. In a deviation much less marked, such for instance as the presence of one more than the normal number of spines in a fin, this ultimate criterion of transmission might fail us even were it practicable to put it to the test. A surer way of determining phylogenetic variation is to measure variation in the bulk by means of curves. If, say one thousand individuals of a definite time and place, show in the aggregate a character different from that normal to the species, it is phylogenetic. Such variations may occur in successive years or at isolated places. The phylogenetic character is in such a case really made up of a large number of ontogenetic variations which must also be capable of reappearing; that is, they must also be phylogenetic. A better way of stating the problem would seem to me to be that:

All variations are ontogenetic, some are at the same time immediately phylogenetic and many if not all may become so—a phyletic series. This leaves open the question of the conditions under which ontogenetic variation becomes phylogenetic and ignores the unchanged germplasm theory which from purely embryological grounds is untenable.

The paragraphs pertaining to this subject in the following direction are: 7. 8, 13, 15, 16.

Nearly synonymous terms with ontogenetic and phylogenetic are the terms variation and mutation as used by Newmayr, Waagen, and Scott. Variation is here applied to locally different forms, while mutation is applied to the chronological changes or "steady advance (of the mean) along certain definite lines" The latter term may for our purpose be still further restricted by applying it not only to the changes of the mean in successive geologic periods, but to the changes in the mean which may occur in two successive years or broods.

To quote Newmayr, pp. 60-61 (from Scott, p. 372), "Weil ein Theil der Merkmale gleichmässig nach einer Richtung im Laufe der Zeit mutirt, zeigen andere Charactere regellose Abänderungen und jede Mutation entwickelt denselben Varietätenkreis." Scott illustrates this process by comparing the mutation to the progress of a cyclone center and the continual circlet of variations to the circulating winds.

DETAILED DIRECTIONS FOR COLLECTING AND STUDYING SPECIMENS.

The following directions and explanations have been prepared for the students at the Biological Station for the study of the variation of the inhabitants of lakes Turkey and Tippecanoe and the small lakelets in the neighborhood.

1. Collect at random all available specimens, to the number of several hundred, the last week in June, in both Turkey and Tippecanoe lakes, keeping the exact location where each lot of specimens was collected.

It is necessary to collect at random or the personal element of the collector may become a disturbing factor in determining the variation. The date, which is not necessarily fixed for any particular week, has been selected because at this time many very young specimens, but a few weeks old, can be secured. It is necessary to collect in both lakes at approximately the same date in order to secure corresponding ages.

2. Collect in the same manner and an equal number of specimens in each lake near the end of August.

From this second collection the rate of growth and any elimination taking place early in life may be determined.

3. Arrange the material of each date according to the size, to determine whether the broods of successive years can be separated.

If specimens have been collected at random and include all sizes this can usually be done for the preceding few years. Among the older individuals the gradation in size is usually too perfect to permit any grouping according to age.

4. Determine the variation in two or more prominent characters in each brood of specimens, keeping the record and labeling the specimens in such a way that the specimen for any record can at any time be re-examined. Determine at the same time the sex.

This is by far the most laborious and time killing operation, but absolutely essential to determine anything further. The characters measured in fishes can always be the number of rays in the dorsal and anal fins, and the number of scales in the lateral line. Other characters will vary with the species, as one species has one, another a different character that lends itself especially to the study of variation. In reptiles deviations in the number and characters of plates are available characters for the study of variation. Of course any character can be taken, but one in which the variation can be numerically expressed and the number be determined by a simple count instead of a measurement, is vastly superior, since nothing can be left to the judgment, and the personal element is therefore much less important.

5. Are there external sexual differences, and is the amount and extent of variation different in the sexes?

This determination can usually be left till later; it is introduced here so as not to mar the sequence of the following points.

6. Is there a successive modification in going from younger to older specimens indicating a structural modification with age?

It may be possible with some species, for instance, that the number of rays increases directly with the age. Should such a case exist it might give rise to entirely erroneous notions as to the influence or effect of selective destruction.

7. Is the variation of each year grouped about a mean common to all the specimens, or is each year's variation grouped about a center of its own?

While the idea of the annual variation or the reaction of each brood to a slightly varying environment was supposed to be a possible element, and suggested as such in my first announcement of the station, I was entirely unprepared for the startling annual variation in such a prominent character as the number of dorsal spines which has been discovered by Mr. Moenkhaus and reported upon in another paper.

The neglect of the consideration of the environment during the early period of development in modifying successive broods in different ways may lead to entirely erroneous ideas of the structural modifications of growth on the one hand, or the entirely erroneous ideas of the action of selective destruction on the other. To determine the latter it is absolutely necessary to take individuals of the same year's broods at successive periods or successive years. Whether as great an annual fluctuation is present in crabs as has been observed in Etheostoma I can not presume to say. But the entire neglect of this element vitiates the results of Prof. Weldon, of the committee of the royal society for "Conducting statistical inquiries into the measurable characteristics of plants and animals," which Mr. Thistelton-Dyer (Nature, Mch., 1895) considers to be "among the most remarkable achievements in connection with the theory of evolution."

I quote from Prof. Weldon to show his methods and results. (Nature, Mch. 7, 1895, p. 149.) "In order to estimate the effect of small variations upon the chance of survival, in a given species, it is necessary to measure, *first*, the percentage of young animals exhibiting this variation; *secondly*, the percentage of adults in which it is present. If the percentage of adults exhibiting the variation is less than the percentage of young, then a certain percentage of young animals has either lost the character during growth, or has been destroyed. The law of growth having been ascertained, the rate of destruction may be measured, and in this way an estimate of the advantage or disadvantage of a variation may be obtained.

In order to estimate the effect of deviations of one organ upon the rest of the body, it is necessary to measure the average character of the rest of the body in individuals with varying magnitude of the given organ."

Conclusions reached by an application of these principles to a study of the shore crab gave as a result that—*a*. There is a period of growth during which the frequency of deviations increases. *b*. That in one case the preliminary increase is followed by a decrease in the frequency of given magnitude, in the other case it was not. *c*. Assuming a particular law of growth the observations show a selective destruction in the one case and not in the other.

8. What is the relation of the annual fluctuation (mutation) in variation to the annual fluctuation in the different elements of the environments?

9. What is the difference in the variation of the youngest brood early in the season and late in the season, and what is the difference in the variation in succeeding years of the same brood? Is this difference, if any exists, due to modifications with age or to selective destruction, *i. e.*, has a larger percentage of individuals with one characteristic been eliminated than of individuals with this characteristic slightly different? In what part of the curve of variation have the greatest changes been produced?

10. If certain individuals with definite characters seem to survive, can it be determined in what way this variation brings about the survival?

11. At what age or stage of growth are variations greatest?

12. Can variations arising with age be referred to habits or environment?

13. What is the relation of sports or saltatory variations to the continuous variation numerically?

By saltatory variations are meant all those variations not connected with the mean by intermediate steps.

14. Are saltatory characters always bilateral? If not, to what degree are they bilateral?

The fact that a saltatory variation is confined to one side or is found on both sides, may enable us to determine whether the deviation began in the germ before the appearance of bilaterality or is of later origin.

15. In how far is the repetition of a character due to the repetition of the environment as shown in the correlation of annual fluctuations in environment with annual variations? See under 8.

Whitman Biological Lectures, 1894, p. 4: "An epidemic of metaphysical physics seems to be in progress—a sort of *neo-epigenesis*. In place of the *vis essentialis* of the old epigenesis, the new epigenesis sets up as its fetich the *vis impressa*. The new god is preferred because it works from the outside instead of the inside. It represents the sum of external conditions and influences at the present moment, and is proclaimed all-sufficient for building up organisms out of isotropic corpuscles. Previous conditions are not, indeed, quite ignored, for they have resulted in special molecular constitutions called germs, and these display molecular activities known as metabolism, growth and division. The long past can bring forth only a molecular basis; a few hours of the present can supply all, or nearly all, the determinations of the most complex organism. Impotent past; prepotent present. We have no longer any use for the 'Ahnengallerie' of phylogeny. Heredity does not explain itself or anything else, and it detracts from the omnipotence and universality of molecular epigenetics. We are no better off for knowing that we have eyes because our ancestors had eyes. If our eyes resemble theirs it is not on account of geneological connection, but because the molecular germinal basis is developed under similar conditions. The reason this basis becomes an eye rather than an ear or some other organ is wholly due to its position and surroundings, not to any inherent predeterminations. If the material for the eye and the ear could be interchanged in the molecular germ, that which in one place would become eye would in the other place become ear, and *vice versa*."

16. In what characters does the same species in the neighboring lakes differ, and in what respects does the variation differ in the different lakes?

17. Are variations in one part of the body correlated with variations in another part of the body?

In many cases this can only be determined by converting the variations in part into the terms of the variation of another part. The method for doing this has been suggested by Galton, whose method is discussed at the end of this paper.

18. What correlation is there in the variation of different species under the same environment?

As far as I am aware, no systematic studies of this description have been made. With us this study resolves itself into the determination of whether the fishes in Turkey Lake all differ from those in Tippecanoe along definite, determined ways, so that given the characters of a species for Turkey Lake the characters for the same species in Tippecanoe could be predicted.

Similar but exotic instances are the absence of ventral fins in some of the fishes inhabiting even widely separated mountain lakes, and the presence of enlarged scales along the base of the anal in the Cyprinidæ inhabiting mountain streams of India; or, to come nearer home, the peculiar color patterns of the fishes in some regions of upper Georgia.

Method of Presenting Results. Results of statistical inquiries into variation can best be presented by frequency of error curves, and these will be used wherever possible. The abscissa will in all cases be made to represent the size of the organ, the ordinate the percentum of individuals having the particular size.

To convert variations in one organ into the terms of another organ the scheme of distribution will be used with the formula given by Galton for comparing one such curve with another. The process of comparing any curve "a" with any curve "b," multiply each of "a's" height by $\frac{\text{Q of "a"}}{\text{Q of "b"}}$ The Q of any scheme of distribution is one-half the difference between any two grades. The same grades in the two curves to be compared being used to determine their Q for this purpose, 25 per cent. and 75 per cent. are suggested as most convenient by Galton.

Ideally the variations occurring in a single organ expressed by a frequency of error curve, when a large number of individuals have been examined, will form a symmetrical curve which is called a "normal." Such a curve may always be expected when the material under consideration is of a single origin and has developed under the same environment. Unfortunately for non-mathematical evolutionists, the converse does not seem to be the case, for a symmetric curve may be made up of two symmetric curves with axes not far apart, a fact that can only be determined mathematically. Says Pearson, "There will always be the problem: Is the material homogeneous and a true evolution going on, or is the material a mixture? To throw the solution on the eye in examining the graphical results is, I feel certain, quite futile."

It is not hoped that the data can be treated with the mathematical refinement suggested by Pearson, nor is it probable that such treatment of our material will become absolutely necessary, since there can be but little question of the unity of origin of the material in any given small lake.

While usually, as stated above, the curve resulting from the study of a large number of specimens will be symmetric, it will frequently be asymmetric. Samples of the different sort of curves actually observed are given.

Asymmetric curves may be the result,

1. Of the selective influence working on one side of a symmetric curve and be then found in more or less mature specimens.

2. Of the reaction to a change in the environment and indicative of a mutation or change in the mean specific form.

3. Of the double origin of the material under consideration, and may then have a great variety of forms, from slightly asymmetric curve to one with a broad top or with many peaks.

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VARIATION OF NORTH AMERICAN FISHES. II.

The Variation of Etheostoma Caprodes Rafinesque in Turkey Lake and Tippecanoe Lake.* By W. J. Moenkhaus.

Introduction.—In a former paper on the "Variation of *Etheostoma caprodes* Rafinesque" (Am. Nat., Aug., 1894), I determined the geographical distribution of this fish and the geographical variation of its color-pattern and fins.

It was found that this species inhabits practically all the fresh waters of the Atlantic slope east of the 100th meridian and west of the Alleghany Mountains. Its northern and eastern limits are the Great Lakes and Lake Champlain; its southwestern, the Rio Grande in the extreme southern part of Texas.

The following conclusions were reached among others:

1. Each river system from which specimens were examined possesses a peculiar variety. This peculiarity is most striking in the color-pattern.

2. All the variations are continuous.

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