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THE RELATIONS BETWEEN THE VARIABILITY OF ORGANISMS AND THAT OF THEIR CONSTITUENT ELEMENTS.

IN a study of the varying forms of organisms we may either direct our attention to the variability of the organism as a whole, or to the variability of its constituent elements. When two organisms differ in form, their differences are necessarily founded on differences in the forms of their corresponding parts, and we are justified in assuming each of these parts as very small. The corresponding parts may consist of homologous cell groups, of individual cells, or of other small homologous elements of the two organisms. These small elements may differ in size and form, and new elements may also be added in the one or the other organism, so that there may also be a difference in the number of elements. The difference between the two organisms may then be considered as a resultant of the differences between their constituent elements. Therefore, there must be a certain definite relation between the variability of the elements and that of the whole organism.

In order to make this clear we will, for a moment, consider the elements as independent units, not as parts of an organic whole. In this case, each element would be entirely independent of the other. When we consider two organisms thus constituted in which the total number of cells is the same, we find that they cannot possess any variability, because the variations of the constituent cells would compensate each other. This can be proven as follows: If we determine the form of an organism by a number of measurements taken in various directions, then each measurement may be considered as made up of many constituent elements. On the average, the variability of the combined elements will be proportionate to the square root of the number of elements, while the value of the total length of the combined elements will be proportionate to their number. If, therefore, the number of elements is very great—and there is nothing to hinder us in assuming each element as very small and their number as very great—the variability of the whole measurement must be very small, according to the small value of the proportion between the square root of the number of elements, and the number of elements. Since this contradicts the fact that all organisms are variable, it follows that the elements cannot be constant in number and mutually independent. This conclusion is obvious from a morphological point of view, but it seemed desirable to point out that the independence and constant number of elements would entail lack of variability in the whole organism.

If the elements were independent of each other but varied in number, we might assume in accordance with morphological observation that each group of elements had a certain limited period of multiplication which proceeds at a definite average rate. Then it may be said that this period undergoes certain changes that are due to chance. If this were the case, the size of the organ would increase approximately in geometrical progression when the period increases in arithmetical progression.

It is probable that, on the whole, the periods of development of various organisms vary around the typical period according to the laws of chance. Then the frequencies of periods belonging to different individuals would be arranged symmetrically around the typical period, while the measurements corresponding to each period and belonging to different individuals would be arranged asymmetrically around the type, in accordance with the relations between size and period. It is quite evident that the observed distributions of variations around a type do not generally conform with a law of this character, and therefore this theory must also be rejected as insufficient, although we recognize that it may explain a part of the general phenomena of variability.

It is, therefore, necessary to assume the elements of organisms to be correlated. This is entirely in accord with the evidence of morphology and of pathology. If the number of elements is assumed as constant, it is easy to determine what the results of such correlation must be. 'Correlation' means that the change in form and size of one element influences more or less the forms and sizes of other elements. Such correlated elements may either be contiguous, or they may be related in some other way. The degree of their relation may be expressed by an index of correlation.

If the correlation of all the elements were perfect, that is to say, if a change in one would necessitate a corresponding change of a certain definite amount in all the others, the variability of the whole organism would be proportioned to the average variability and number of the homologous elements. This condition is as unlikely as that of complete independence of the elements. We must draw the conclusion that the variability of the organism as a whole will always be less, in proportion to its size, than the variability of its constituent elements; or, as we might perhaps say, the variability of the individual cells that constitute an organism must always be greater than the variability of the whole organism.

It may be well to illustrate the effects of correlation by assuming simplified conditions of correlation.

Assuming first, that the elements may be classed in a limited number of groups, each consisting of interdependent elements, so that the enlargement of one element of each group would necessitate a definite amount of enlargement of all the others. Furthermore be it assumed that the chances of a small number of these groups being enlarged are subject to accidental causes. Then the probability that one, two, three, or more of these groups are affected can be calculated according to the binomial law. Each group would contribute a definite, invariable amount to the total variability and the general variability would, therefore, also conform to the binomial law.

We will next assume a case which is somewhat nearer natural conditions. When we count and measure the total number of elements in *all* the individuals of a variable series, we obtain certain definite numbers of elements of various sizes and we can express numerically the frequency or probability of each size. In order to simplify matters, we will speak only of elements of decreased size and of enlarged size. The proportion of these two classes is definite in the total number of elements belonging to the different organisms of the series. If inside of each organism there were no correlation, then the proportion of large and small elements in each organism would, on account of the great number of elements, correspond to their proportions in the whole mass of elements. On account of the existence of correlations in each organism the occurrence of each enlarged element will have the effect, that an additional number of enlarged elements may be expected in the same organism, and the occurrence of an element of decreased size will add to the probability of elements of this character in the organism in which it occurs. The arrangement of these elements becomes, therefore, similar to that in a mechanical mixture of elements of two sizes, which are not uniformly distributed, but in which large and small parts cluster together. It is quite clear that the variability of distribution in such a mixture must be quite different from that found in cases of even mixture. It will depend entirely upon the distribution of large and small elements, and the number of elements of both classes that are found in a unit of space, how their proportion in each unit of space will vary.

We may obtain an insight into such variabilities by a consideration of the results obtained by taking a certain number of contiguous balls out of a row containing large and small balls that are not thoroughly mixed. The two arrangements given under 1 and 2 may serve as examples:

1. ● ● ● ● • • • ● ● ●

2. ● ● ● • ● • • ● ● ●

If four contiguous balls are taken out of each of these rows, we find that in the drawings made from the two series large balls occur as follows:

	Series 1.	Series 2.
4 large balls	1 Time	0 Times
3 " "	2 Times	3 "
2 " "	2 "	3 "
1 " ball	2 "	1 Time

Evidently, the distribution in cases of this kind cannot be foretold. This result may be expressed in a more general form as follows: If only one series of elements of an organism are interdependent, and all the others independent, the variability of form of all the individuals will depend primarily upon the distribution of disturbances in the interdependent elements in the whole series of individuals. Therefore the distribution of variations cannot be foretold. The same is true if the number of groups of interdependent elements is small.

When, however, the number of these groups of interdependent elements is somewhat greater and each group of correlations is independent of the other, then the conditions approach again those described before, when we assumed a number of groups in which the size of one element of a group determines the sizes of all the other elements of the same group. We may then expect to find a distribution the type of which is determined by the binomial law, because the combinations of groups that occur in each individual are determined by this law, while the law must be modified by the variability of the size of each correlated group, taken as a total. It is quite evident that the resultant curve must be similar in its general character to the series of binomial points, but continuous on account of the variability of each group. This phenomenon is still further complicated by the variation in the number of elements, the effect of which was discussed before.

We may reach the same result by assuming that the form of the whole organism is affected by a limited number of causes variable in intensity, each of which influences to a measurable degree the form of the organism. The combination of such groups of independent causes, limited in number and each having measurable results will bring about a distribution of variations of the same character as the one described before. The phenomenon, expressed in this manner, does not differ from the expression found before, because it does not seem probable that each cause would affect all the elements comprising the organism in the same manner. It seems much more likely that certain groups of elements will be affected more by one cause than by another. At the same time, it is possible that the same element may be subject to several causes and thus belong to various groups of correlated elements. Karl Pearson's discussions have shown that many distributions can be explained satisfactorily by assuming that they correspond to a continuous function determined by the points binomial.

It will be noted that, on the whole, the greater a variable measurement, the more nearly will the distribution of variations be symmetrical and in conformity with the exponential law. This may be expected, because the greater the measurement, the greater will probably be the number of independent, correlated groups. The increase of their number necessitates an approach to the exponential law. On the other hand, the smaller the measurement, the more probable that a great part of its constituent elements are subject to the same causes, so that the conditions are favorable to the combination of a small number of independent causes, each of which brings about considerable variation, so that we may expect as a resultant skew distributions of variations.

It would seem, therefore, that the whole range of phenomena of variability can be understood on the basis of our conception of the relations between the variability of the small constituent elements of an organism and the variability of the organism itself. We are justified in drawing the following conclusions:

1. The elements of organisms are more variable than the organisms themselves.

2. The elements of organisms vary in correlated groups.

3. The characteristics of the variability of an organism depend upon the correlations of its constituent elements, so that a knowledge of these correlations will enable us to determine the characteristics of the variability of the organism.

It follows from this that the problem of variability may be treated by a study of the variability and of the correlations of the constituent elements of organisms. The study of physiological and pathological variations that elucidate correlations will, therefore, be a most powerful factor in the discussion of the problem of variability.

This point of view coincides closely with that of Rudolf Virchow who has always emphasized that the clue for the problems of variability must be looked for in the study of cellular variation.

Under certain simplified assumptions the problem, as here defined, may be made amenable to statistical treatment. If all the contributory causes of variation are given equal weight, and if it is assumed that the index of correlation for all the groups is the same, then it is only necessary to determine four unknown quantities: the total number of causes (or correlated groups); the probable number of causes (or correlated groups); the amount of influence of each cause (or correlated group) upon the whole organism; the variability of the effect of each cause (or correlated group) upon the whole organism. These few data can be calculated without any great difficulty from the averages of the first four powers of the individual variations. This method may be serviceable as long as the actual correlations are unknown.

Still another conclusion may be drawn from our considerations. We have seen that the variability of an organism depends upon the correlations of its elements, and that the variability must be the greater the closer these correlations and the less the number of correlated groups. At the same time, the variations will be the more likely to have skew distributions, the less the number of correlated groups. A disturbance in one element of an organism thus constituted must, therefore, result in a considerable variation of the whole. That is to say, that in the case of skew distributions of variations we may expect sudden transformations of type due to small causes. In organisms in which the variability is symmetrical, we may generally expect the whole form to be controlled by many independent causes, or by many independent groups of correlated elements. In this case, the changes of form due to small changes of conditions will probably be less marked.

The principal advantage of the method of considering variation that has been here suggested is that the occurrence of variations in fixed lines, that are so difficult to understand, may be considered as a result of chance variation of small elements and of physiological correlation. Both of these are much more readily understood than a variation of form that does not show any immediate relation to the causes producing the variation.

It has often been asserted, or assumed, that skew distribution of variations is a proof of the effect of selection, or of some other kind of instability of type. Our considerations have shown that this is not necessarily the case. Skew distributions may be found in stable forms. On the whole, it does not seem possible to discover by purely statistical methods the causes of skewness. The numerical material obtained by measurements can be made to fit satisfactorily many theories that would account for the skewness. It is necessary to base such theories on biological investigations and to subordinate our statistical methods to the biological point of view. Otherwise the result of statistical inquiry will be of little use and may even become quite misleading.

FRANZ BOAS.

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*ON THE TRUE NATURE OF TAMIOSOMA.**

IN 1856 the late T. A. Conrad described a remarkable fossil from California, under the name of *Tamiosoma gregaria,* composed of large tubes with a longitudinal cellular

* Communicated by permission of the Director of the U. S. Geological Survey.