There will also arise, I believe, in a work of this kind, a necessity for distinguishing between the essential characters of a group and those characters which are used by the systematist merely to enable students to recognize members of the group. For it seems to me that the essential characters of a group of organisms do not lie necessarily in the presence or absence of any structure or structures, or in the form or any part or parts of the body of the living members of the group; but rather in the characteristic structure of the progenitor of the group, and in the direction of specialization of the descendants of this progenitor.

The recognition-characters are those usually first observed by the investigator, and are those commonly given in taxonomic works. In many cases these recognition-characters are also essential characters, especially in the case of groups that have been thoroughly studied. But by the taxonomic methods now commonly used, search is chiefly made for recognition-characters. The more skilled the systematist the more likely is he to discover and use as recognition-characters those that are really essential, although the distinction pointed out here may not be recognized by him.

Very likely we shall not abolish the present systems of nomenclature and description in the larger units, but we shall modify and extend them. We shall break away from the old lines of cleavage. We shall learn what marks that are correlated with function can be used as expedient diagnostic characters. We shall make an increasing effort to use absolute characters, not merely relative and comparative ones. We ought to make the 'type' of the species the real biological or phylogenetic type, not cling merely to the 'original' specimen that chanced first to be named. What we now call 'types' may be wholly unusual and even non-significant forms. If the book or literary type is in time to be the real type, then we shall re-group our species-units, and this will be the greatest possible gain.

If we decide that literary-species must come, in the future, to correspond to the physiological or elementary species, then we may hope to express the direction of evolution fairly well in our taxonomic schemes. These taxonomic schemes must proceed centrifugally and dichotomously rather than lineally. They must arrange about foci. I wish to quote again from Comstock:

If the history of a group be worked out in the manner indicated, the student will feel the need of recording his results in such a way as to indicate the phylogeny of the divisions of the group. But as the necessities of book-making require a linear arrangement of descriptions, this is somewhat difficult; for the natural sequence of groups should be represented by constantly branching lines rather than by a single straight line.

It seems to me that the most practicable way of meeting this difficulty is to begin with the description of the most generalized form known, and to follow this with descriptions of forms representing a single line of development, passing successively to more and more specialized forms included in this line. When the treatment of one line of development has been completed, take up another line, beginning with the most generalized member of that line and clearly indicating in the text that a new start has been made.

In making the foregoing suggestions I am well aware that I have not devised any definite nomenclatorial or taxonomic schemes by which they can be carried out. I doubt whether it is worth while to devise any schemes. We need only to establish a few principles and to look upon the present methods as temporary, allowing new methods to grow as our ideas grow. There can be no finality in such schemes or systems. We have lately seen a vigorous revival of the effort towards 'stability' of nomenclature; but nomenclature is only a bit of language, and language can never be stable if it is vital. It was the old idea that systematic work is for the purpose of making record; it is the new idea that it is for the purpose of expressing the meaning of the organic creation.

Ethology and the Mutation Theory: WILLIAM MORTON WHEELER, Curator of Invertebrate Zoology, American Museum of Natural History.

"The mutation theory," as we learn

from the opening sentences of de Vries's celebrated work, "asserts that the characters of organisms are built up out of units distinctly different from one another. These units may be combined to form groups, and in allied species the same units and groups keep recurring. Transitions, however, such as are so abundantly represented in the outer forms of plants and animals no more occur between these units than between the molecules of chemistry." It follows as a corollary from this statement that species must be conceived to arise from preexisting species by discontinuous variations, or mutations, and not by fluctuating variations, or variations proper. The theory is built on a number of remarkable facts derived from breeding organisms, with special attention to their morphological characters or attributes. I have been asked to consider the question as to whether the theory will apply also to the behavior or ethological, as well as to the morphological, aspect of organisms.

The biologist finds it well to distinguish carefully between structure and function, just as the psychologist finds it greatly to his advantage to distinguish sharply between the psychic, on the one hand, and the physiological and morphological, on the other. For the purposes of discussion I will take the standpoint of the biologist in so far as it relates to the distinction between structure and function, but I will combine under function both the physiological and psychological aspects as together constituting ethology, at any rate to the extent that they are involved in the behavior of organisms.

Now, inasmuch as ethology deals with processes, or phenomenal diversity in time, whereas morphology deals with the spatial diversity of phenomena, it is evident that ethological must be very different from morphological characters. It might even be said that the ethologist has no right to speak of a process as a character or characteristic, and the original Greek meaning of these words would seem to limit their use to the structural configurations resulting from specific acts or processes. This need not prevent us, however, from extending the meaning of the terms to include also the typical and specific reactions of the organisms to their environment. Certainly in the case of the human species, which is best known ethologically, the terms character and characteristic are hardly used of physical structures, but almost exclusively of typical modes of activity.

In its application to ethology the mutation theory can only mean that organic species must differ from one another by discrete idiosyncrasies of behavior. Most biologists would probably regard any discussion of mutation from the ethological standpoint either as superfluous or as necessarily and merely confirmatory of the results of morphological study. In their opinion it would follow as a matter of course that the functional and ethological characters of organisms must fluctuate or mutate according as the structural characters vary continuously or discontinuously. In my opinion this is not so self-evident as it would appear to be at first sight.

It is true, of course, that the various structural categories from the phylum down to the species, subspecies, variety, sex and individual—all show what may be regarded as correlated or corresponding ethological characters, although this correspondence is often very loose, vague and irregular, for it is evident that slight morphological may be correlated with complex ethological characters, and conversely. Some such correspondence may also be observed in hybrid forms. All this is usually taken for granted, and as a consequence the theory of an ethophysical parallelism, on the model of the famous psychophysical

parallelism seems to have been tacitly accepted by many biologists. If we follow up the matter, however, we soon find that in the field of possible observation the ethological tend to outstrip the morphological characters. We observe great differences in habits and behavior between genera of the same family, between species of the same genus, and what is most significant, between individuals and even twins of the same species. At the same time we may be utterly unable to point out the corresponding structural differences, which, according to any theory of parallelism, should accompany such pronounced ethological distinctions. What bold man, for example, will undertake to show us the morphological characters corresponding to such striking differences in behavior as are manifested by the horse and the ass, by cats or dogs of the same litters, or children of the same parents? Of course, we are at once reminded that there must be corresponding morphological differences represented by cell-structures, biophores, ids, complex chemical compounds, etc. We are compelled to admit that these may exist, but until a function can be shown to be correlated with a particular structure, the structure is, of course, to all intents and purposes a purely hypothetical and imaginary entity. It is clear that the prestige of morphology has been artificially enhanced by a continual appeal to complex invisible structures. Whatever may be the truth concerning such structures, it is undoubtedly a matter of considerable theoretical and practical importance that we are able to detect ethological where we can not detect morphological differences or characters.

We may, in fact, be permitted to reverse the matter and take the point of view of the psychologist and metaphysician rather than that of the morphologist. In other words, we may start with behavior or the dynamic, *i. e.*, physiological and psychological processes of the organism, and regard the structure as their result or objectivation. The organism makes itself—the *ethos* is the organism. In this sense the honeycomb is as much a part of the bee as is her chitinous investment, and the nest is as much a part of the bird as her feathers, and every organism, as a living and acting being, fills a much greater sphere than that which is bounded by its integument.*

Although the time is so very limited, permit me to digress somewhat further on a more practical consequence of the view here advocated. We are certainly justified in regarding ethological characters as very important, as belonging to the organism and as being at least complementary to the morphological characters. If this is true, our existing taxonomy and phylogeny are deplorably defective and one-sided. To classify organisms or to seek to determine their phylogenetic affinities on purely structural grounds can only lead, as it has led in the past, to the trivialities of the species monger and synonym peddler. This has been instinctively felt by all biologists whose development has not been arrested in the puerile specimen-collecting stage.

* Compare, in this connection, the following passages from Schopenhauer's well-known essay on Comparative Anatomy (Ed. Frauenstedt, Bd. 4, pp. 45 and 58): "Man betrachte die zahllosen Gestalten der Thiere. Wie ist doch jedes durchweg nur das Abbild seines Wollens, der sichtbare Ausdruck der Willensbestrebungen, die seinen Charakter ausmachen. * * * Aus meiner Lehre folgt allerdings, dass jedes Wesen sein eigenes Werk ist. Die Natur, die nimmer lügen kann und naiv ist wie das Genie, sagt geradezu das Selbe aus, indem jedes Wesen an einem underen, genau seines Gleichen, nur den Lebensfunken anzündet und dann vor unseren Augen sich selbst macht, den Stoff dazu von Aussen, Form und Bewegung aus sich selbst nehmend; welches man Wachsthum und Entwickelung nennt. So steht auch empirisch jedes Wesen als sein eigenes Werk vor uns. Aber man versteht die Sprache der Natur nicht, weil sie zu einfach ist."

Embryology, by no means a purely morphological science, but one daily assuming a more physiological aspect, has come to have a weighty voice in matters of classification. More recently chorology, or biogeography—a distinctively ethological science—has come to play an equally important part. And rightly, because the organism may be said to seek, and in many cases even to make, its own environment. Every field naturalist knows that he is frequently guided to the more delicate specific and varietal distinctions, not so much by the structural differences between the organisms he is observing, as by differences in their habitat or behavior. Then closer scrutiny may often, although not always, reveal correlated structural differences. When such structural differences are not to be detected we speak of ethological species, and the number of these is undoubtedly much greater than was formerly supposed.* The great reliance on geographical distribution in the more refined taxonomy of certain groups of organisms, like the birds, mammals and social insects, shows an ever-deepening appreciation of ethological characters. It is even jocosely asserted that certain mammalogists are quite unable to identify a specimen unless they are first informed of the exact fence-corner in which it was trapped. Then, and not till then, are they able to perceive the delicate specific or subspecific shade of pelage which goes with life in that particular corner.

The fact that the morphologist has so consistently either neglected or opposed the use of ethological characters in classification shows very clearly that in his heart of hearts he has never very earnestly concerned himself with the parallelism of structure and function. He is inclined to regard function, especially psychical function, as something utterly intangible and capricious. For does it not seem to make its appearance in the embryo or young *after* structure has developed, and to depart at death before the dissolution of visible structure? And are not our museums largely mausoleums of animal and plant structures which we can forever describe and redescribe, tabulate and retabulate, arrange and rearrange, without troubling ourselves in the least about anything so volatile as function?

It is, indeed, not only conceivable, but very desirable, that a taxonomy should be developed in which the ethological will receive ample consideration, if they do not actually take precedence of the morphological characters. It is certainly quite as rational to classify organisms as much by what they do as by the number of their spines and joints, the color of their hairs and feathers, the course of their wing-nervures, etc. To regard our existing purely structural classifications as anything more than the most provisional of makeshifts, is to ignore the fact that the vast majority of organisms which they are designed to cover are known only from a few dead exuviæ. There are, of course, enormous difficulties in the way of constructing ethological classifications, quite apart from the fact that our knowledge of behavior is even more fragmentary than that of structure, as any one will realize who tries to write an ethological description of some common animal or group of animals. In morphology the elements of description can be treated as parts of an orderly and traditionally respected routine, but in ethology we still lack the necessary preliminary analysis of the more complex instincts, and are therefore unable to construct uniform and mutually comparable

* I have in mind a number of cases among insects, such as certain species of ants. There are American forms of the genera *Pheidole, Myrmica, Myrmecocystus, Formica*, etc., which exhibit geographical differences in habits without perceptible morphological differences.

descriptions. One great desideratum in ethology at the present time is a satisfactory and sufficiently elastic working classification of the instincts and reactions, like that of the organs and organ systems of the morphologist. Such a classification can be developed only by comprehensive, comparative study of behavior in a number of genera and families and not by any amount of intensive study of a few reactions in a few species.*

It seemed necessary to discuss ethological characters at some length for the purpose of vindicating their importance. Having attempted this, I may say that these characters seem to me to offer even fewer difficulties than the morphological characters to the acceptance of the mutation theory, for the reason that the ethological and psychological processes are conceived primarily as qualities and not as quantities. Thus the psychical elements, *i. e.*, the simple feelings, cravings and sensations, are disparate qualitative processes which can not be derived from one another or from some more undifferentiated process. This is still more evident in the case of the complex psychical phenomena. Similarly, instincts, with which ethology is most concerned, when resolved into their simplest components are seen to consist of discrete reactions which can not be shown to arise from one another. Although, on the other hand, the measurable intensities and durations of the reactions are analogous to the fluctuating structural variations, it is even more difficult for the psychologist to conceive of a particular feeling, craving or sensation as arising from the greater or less intensity or duration of some other psychic process, than it is for the morphologist to conceive of the origin of new characters from the fluctuating variations of structure.

It is, of course, extremely difficult to determine the first inception of an instinct process, as one may point to the mutational inception of a structural character. An instinct is not an isolated manifestation, but is always more or less influenced by or inextricably bound up with other instincts. Nor do we know of any instinct which manifests itself only in a single species. Still there are numerous cases in which we seem to see more or less clearly the phylogenetic change from one instinct to another. Take, for example, the change from a flesh-eating or insectivorous to a granivorous or vegetarian instinct, a change which has undoubtedly taken place many times in the animal kingdom and is still taking place, especially among insects, birds and mammals. The organs which are useful in obtaining, comminuting and digesting animal food will function with a certain degree of efficiency when vegetable food is substituted, and the animal can pass either at once from animal to vegetable food or through a stage in which both kinds of food are eaten. In the latter case, only after the transition has been completed can we suppose that the organs will begin to assume the more perfect structural adaptations to a vegetarian diet. The state in which the animal is both carnivorous and vegetarian may be regarded as one in which two instincts coexist, and the purely vegetarian is reached by the mutational acquisition of a new and the mutational loss of an old instinct. Undoubtedly many changes of instinct are brought about in this manner so analogous to what has been called in morphology the 'substitution of organs.'

Mutation is even more urgently demanded for the explanation of many other instincts, especially those of symbiotic and parasitic species and of species with pro-

* An avowedly provisional but elaborate 'System der thierischen Triebe' was suggested several years ago by G. H. Schneider in an interesting work ('Der thierische Wille,' Leipzig, Ambr. Abel, 1880), but subsequent workers have not even adopted, to say nothing of having perfected, the schema.

found and sudden metamorphoses. In these cases a particular activity, on which must often depend the life of the individual or of its progeny, has to be performed with a high degree of proficiency at its very phylogenetic inception or it can be of no advantage to the individual or the race. Such cases, with which you are all sufficiently familiar, have ever been the insurmountable obstacle to the evolution of instincts on the theory of fluctuating variations and natural selection. The theory of organic selection seems to me merely to conceal but not to overcome the difficulties. The mutation theory frankly avoids the difficulties even if it fails to throw any light on the origin of the mutations, and bundles this into the germ-plasma. It is, of course, no objection to the theory that it leaves something under the heavens to be accounted for. This is rather to be regarded as one of its chief virtues. As working naturalists we have reason to be most suspicious of the theories that explain everything.

*Discontinuous Variation and the Origin of Species:** Dr. D. T. MacDougal, New York Botanical Garden.

That distinct and separate qualities expressed in recognizable external characters may appear suddenly, or disappear completely, in a series of generations of plants, has been a matter of common observation so long that it would be difficult to hunt out and fix upon the first instance of record.

The significance of such phenomena was obviously beyond the comprehension of the earlier botanists, and it is evident that a rational recognition of the phylogenetic value of sports and anomalies necessarily awaited the development and realization of the conceptions of unit-characters, of the minute structures which are the ultimate bearers of heredity, and of the interdependence of the two in such manner as to constitute actual entities as embodied in Darwin's pangenesis, de Vries' intra-cellular pangenesis and in Mendel's investigations upon heredity. It is equally apparent that a proper interpretation of the facts in question, and their distinction from the results of hybridization were possible only by means of the analysis of the collated results of observations upon series of securely guarded pedigree-cultures, in which the derivation of all of the individuals of several successive generations had been noted. For it is now thoroughly realized that the main questions of descent and heredity and of evolution in general are essentially physiological, and as such their solution is to be sought in experiences with living organisms and not by deductions from illusory 'prima facie' evidence, which has been so much in vogue in evolutionary polemics, nor by 'interpretations of the face of nature' with the accompanying inexact methods and superficial considerations. It was upon the safe basis of the first-named conceptions, and by means of the methods entailed, that de Vries so successfully grappled with the problems involved in the investigation of the part played by discontinuous variation in evolution.

In view of the amount of orderly and well-authenticated evidence now at hand, it may be regarded as demonstrated that characters, and groups of characters, of appreciable physiological value, originate, appear in new combinations or become latent, in hereditary series of organisms, in such manner as to constitute distinct breaks in descent.

This is the main thesis of the mutation theory—the saltatory movements of characters, regardless of the taxonomic value of the resultant forms. That the derivatives

* See also, MacDougal, D. T., 'Discontinuous Variation and the Origin of Species.' *Torreya*. 5: Jan., 1905. Pp. 1–6.