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THE DIFFERENTIATION OF SPECIES[1]

WITH the lapse of another year, it is again my privilege and my obligation to present what is technically known as a "presidential address." This occasion is one of particular personal interest, for it marks the close of continuous active service to the academy throughout a period of more than three decades, during which it has been my privilege to serve in almost every designated capacity. And with the close of this evening, I shall pass to the long and venerable list of ex-presidents, however unworthy that association may be with the notable men of science of our community who have directed the life and work of our institution.

A choice of subjects is inevitably controlled by circumstances; the topic must be general in scope, it must be of timely interest, and it ought to be one with which the speaker is familiar, at least to some extent. I have chosen to discuss briefly some aspects of evolution. No other is more comprehensive or more fundamental. Each of the natural sciences, with its own materials and by its own methods, has demonstrated the reality of incessant change, in the heavenly bodies, in mountains and seas and continents, and in the wide array of plants and animals that constitute the organic world.

The further circumstance determining this choice is the fact that for more than twenty odd years I have been engaged in the study of a definite group of animal organisms in an effort to understand the processes by which evolution comes about in wild nature. The natural history of animals is like that of plants, and hence this topic is directly related to botanical generalization. It is of real concern to the geologist also, who, as paleontologist, must deal with the bygone organisms that have lived and have passed away. It is axiomatic, of course, that the student of fossil species can not observe directly the dynamics of specific evolution; what he may know about the actual processes of transmutation can be learned only by the study of existing organisms and their changes, which he then projects into the past—precisely as the geologist can not see his age-old strata in process of

[1] Address of the retiring president, delivered at the annual meeting of the New York Academy of Sciences, December 19, 1927. Photographic illustrations of topographic features, specimens and tabulated statistics, which were employed at the time, are necessarily omitted here.

actual formation, although he can understand their origins from what he now observes in the way of erosion, deposition, solidification and uplift.

The material with which I shall deal specifically consists of certain land-snails that dwell in the larger and higher islands of the western and southern Pacific Ocean. They belong to various and varied species of the single genus Partula. In the course of the past twenty years more than 150,000 individuals have been secured in several groups of islands. As the adult animals are viviparous, the young dissected from the brood-chambers of their parents afford valuable data for heredity. The young number about 250,000. Hence the material comprises an ample array of over 400,000 individuals for the study of distribution, variation, heredity and organic differentiation—which last phrase means evolution.

Last year I presented a general description of these animals and their local distribution, showing how each group of islands bears its own characteristic species, and how each island of a single group is inhabited by forms that occur nowhere else. Indeed, in some instances a given species is confined to a single mountain peak or to a restricted area not more than a hundred yards in any diameter. From such facts of distribution, and from the correlation between geographical proximity and specific similarity, it is possible to decode the history of organic differentiation by which the present situation has come about. And incidentally it was shown also how the zoogeographical data are valuable for the purely geological problem of a pre-Pacific continent.

On this occasion, employing the identical facts of Partula nature and distribution, I purpose to discuss some other aspects of the problem of organic differentiation, and to express some of the convictions that have gained form and definition in the course of the detailed studies of an unusual wealth of material. No claim is made that my conclusions are original or novel, for their like are to be found in commentary and controversial literature. But even at this date in the discussion of evolutionary dynamics, conflicting views are presented to us, more often on theoretical grounds than on the basis of an analysis of organic variation in nature. The Partula work is concrete and circumstantial, and its results make it possible to present definite statements regarding many of the controverted questions of evolutionary procedure.

In particular, the topics are, first and principally, the concept of species, and the change in focus that I believe to be essential if progress is to be made in the analysis of the origin of species in nature; the second is the Darwinian formula of natural selection, and the precise form of its statement that holds for the history of Partula evolution, particularly as regards the problems of utility and the survival value of small congenital variations. The third topic, to be dealt with very briefly, is the opposition of fortuity and orthogenesis. A final profession of evolutionary faith will conclude the discussion.

Our present concept of a species is a heritage from the eighteenth century. It has been useful, and indeed indispensable for the organization of biological information, but at the same time in some ways it has deterred progress in analyzing and understanding the modes by which diverse organic types have come into existence. In medieval times the concept did not exist as such, until with the era of Suarez the evolutionary views of earlier centuries, sanctioned and expounded by the orthodox fathers of the church like St. Augustine and St. Thomas Aquinas, were cast aside in favor of the dogma of supernatural creation, according to which, once for all time, all kinds of living creatures came into being in the Garden of Eden, unchanged and unchangeable. Yet the special creationists themselves were by no means in agreement as to the natures and numbers of organisms thus first constituted. According to some, like Bory de Saint Vincent and Gmelin, the original kinds were what would be called to-day the generic types—Felis, Canis, Homo. As time passed, by natural resolution, each of these was supposed to be divided up into lesser components, such as the species, *Felis leo, Felis tigris,* etc. Others, like Ray and Linnaeus, held that the latter were the primary types; and while at first Linnaeus contended that these had undergone no organic diversification since their creation, later he espoused the belief that transmutation within species had produced different varieties or sub-species. Again, Jordan held that these lesser units—the varieties—were the original things and that a species was an arbitrary aggregate, precisely as a Linnaean genus was a convenient collection of essentially similar types, assembled by convention.

During this period, when the idea of supernatural creation held sway, there was no problem of the *origin* of species, for the various kinds were postulated *ab initio,* just as in embryology the false preformationist views of Bonnet and Haller excluded the problem of embryological differentiation. Such a concept could not have other than a baneful effect upon investigation, for whatever allowance was made for transmutation within genera or within species, this was regarded as quite subordinate to the supernatural fixation of the first-formed kinds, and a general program of organic evolution was impossible.

With Darwin and his work, the whole matter entered its modern phase, when universal organic transmutation came to be fully established, and when the species came to be understood as an artificial concept, like the concept of genus, of order, of family and of class. It is true that the Linnean form of the idea still controlled taxonomy among the major divisions of biology, and it still rules evolutionary discussion to an extent which many, myself included, hold to be unjustifiable and harmful. It is impossible to outline the true conception of species more clearly than in the words of Darwin himself, and while the correct idea is now axiomatic, we must not forget that this was by no means the case when Darwin wrote. He says:

> Certainly no clear line of demarcation has as yet been drawn between species and sub-species—that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at, the rank of species: or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other by an insensible series; and a series that impresses the mind with the idea of an actual passage.
>
> Hence I look at individual differences, though of small interest to the systematist, as of the highest importance for us, as being the first steps towards such slight varieties as are barely thought worth recording in works on natural history. And I look at varieties which are in any degree more distinct and permanent, as steps towards more strongly-marked and permanent varieties; and at the latter as leading to sub-species, and then to species . . . A well-marked variety may therefore be called an incipient species . . .

Here we have a definite statement that a species is only one term in an array of assemblages of lesser or greater comprehensiveness and scope. To focus attention on just that degree of difference which by convention is taken to be specific in degree is no more helpful than to concentrate on the greater degree of difference between two genera or two families. In fact, it diverts attention from the point where the enquiry into the origin of diverse organic types must begin, namely, the production of the individual variant itself, and the passage from parent to offspring. For here, and here only, can the dynamics of organic differentiation come under direct observation. Anything else is deduced. It is admitted, of course, that comparative morphology, crystallized into taxonomy, must take some conventional degree of difference from which to work, and on account of the historical strength of the species idea, it starts with what *on detailed analysis* proves to be a relatively large and a derived degree of difference. From this, it works mainly upwards to genera and to larger groups. But when it proceeds downwards from the same point, namely, to varieties, subvarieties and ultimately to individual variants, it is working in the direction opposite to that of natural organic differentiation.

For purely descriptive purposes, in my own work, it has been necessary to start with the individual variants, and to establish groupings below variety which have the same relation to subspecies as that of subspecies to species, species to genera and so on. All individuals that are alike in at least one distinguishable quality, however they may differ in others, constitute what I call a *gens*—a name that is closely similar to the word gene of the geneticists, and the similarity in name correctly implies that the identical manifest qualities are due to similar genetic factors. Aggregates of *gentes* form a *cohort*—a more inclusive grouping with greater intrinsic diversity than the *gens*. *Cohorts* constitute a *socius*—that is, a geographically outlined assemblage built up of the lesser components. Several *socii,* or indeed a single *socius,* may present a complexion that is collectively distinctive, and hence, they, or it, will form a *variety,* or better a *primary variety,* still more comprehensive and with a still greater diversity among its members. Such *varieties* constitute the *species,* and the rest follows according to convention.

It may sound paradoxical, but it has become increasingly evident to me in prosecuting my own work, that little if any understanding of the *origin* of diverse organic types can be gained through the study of genera, species or even varieties, *after* they have arisen. We can gain knowledge of their evolutionary connections, it is true, on the principle that the degree of likeness is an index of the degree of genetic relationship, for there is no known reason for organic similarity other than common ancestry. But the factors that have made varieties dissimilar, species more unlike, and genera still more so, are not there to be discovered. Let me repeat that we must concentrate on the initial episode when individual offspring present themselves as something different from their parents. What happens when gentes come to differ within their cohort, cohorts within their socii, varieties within the species and species within their genera, is universally the same, and it is nothing but the initial episode repeated again and again.

The conclusion at which we arrive therefore is in effect that the geneticists and they alone are working on the fundamental dynamics of organic differentiation. With the conjunction of Weismannian cytology and Mendelian experimentation a new era was begun, and its accomplishments in the brief period of

twenty-five years are known to all. Now, I believe, we require the same kind of combination of effort, on the part of geneticists who work in the experimental garden and laboratory with complete control of conditions, and of what might be called the analytical taxonomists, who deal with organisms in open nature. Having the assured principles of genetics, the field-worker is justified in postulating an internal genetic control of his minor variations exactly like that which manifests itself in the succession of changing laboratory generations, just as a pair of qualities that are newly found to Mendelize may confidently be referred to chromosomal direction, even though the cytological demonstration in question may not have been made.

So far as the material of Partula is concerned, the elementary episodes of organic differentiation that have been demonstrated, and the long history of evolution rewritten by deduction, reveal no primary or originative factors at work other than those of congenital nature and location. Thus the results are in full accord, with those of laboratory genetics, which allow for external control of the behavior of qualities, it is true, but find no evidence that external conditions actually originate new qualities as such. Despite the fundamental importance of this subject, this brief statement is all that can be given in the present connection.

And now a few words regarding mutation and the supposed conflict between the doctrine of mutation and Darwin's views. The antithesis in question, for which De Vries is largely responsible, has long since disappeared from the only writings that deal directly with the facts, namely, those in the field of genetics. Nowadays the word mutation is used to apply to any congenital departure or variation, whatever it may be in degree. Its real antithesis is a change due to the operation of an external influence, or a somatic modification, sometimes named a fluctuation. Numerous instances of true mutations have been discovered in Partula and in numerous species. Sometimes the new type is rare, like the sinistral mutants in *P. taeniata,* where they number only four out of sixty thousand individuals. Sometimes the novel condition is more frequent, as in many of the color-varieties, or cohorts. These instances prove to be true mutations, for some among the embryonic offspring repeat the new parental character and thus carry it over to posterity.

We come now to the second topic, natural selection, and the way natural selection enters into the evolutionary history of the Partula material. To forestall any possible misapprehension later, let me state at once that I hold myself to be a true believer in orthodox natural selection. Darwin clearly separates this from congenital variation and takes the latter as given, so to speak. Others of the neo-Darwinian school attempted to expand natural selection so as to make it originative in effect as well as discriminatory, notably those who propounded the theory of germinal selection. As to the truth of the elements of natural selection, there can be no two opinions. Given the fact that congenital variations do arise universally, it is found that in general organisms multiply at an excessive rate, and they are thus plunged into some sort of struggle for existence; the unadapted perish, and thus the only ones to carry on are those which are predestined to succeed by their congenital make-up. The crucial point in the whole formula is the matter of the survival value of small differences. Darwin himself did not insist on the positive utility of such individual differences, for he discusses at length a whole series of what he calls "indifferent characters." But Wallace took the extreme position and argued that whether the observer can or can not discern just how a small difference may have been useful, yet it must have been so, else the possessor could not survive. This really begs the whole question. Of course the literature is full of citations of directly useless and eliminative characters that are congenital in origin as mutations, such as the lethal factors in Drosophila and the uni-sexual organization of some of De Vries' primroses. But an unprejudiced review of the many individual differences displayed by the Partulae, whether they be small or large in degree, finds no reason to believe that they are of direct benefit to their possessors, or otherwise. The statement that congenital variation *must not be inutile* or detrimental has really the correct form, as I believe; and I do not regard it as any less Darwinian than any other element of the doctrine of natural selection.

The third topic—fortuity *vs.* orthogenesis—must be dismissed with very brief consideration. There is no evidence that the variations in the Partula material have proceeded along orthogenetic lines, while all the evidence is to the contrary effect. It is not possible here and now to present the detailed facts which warrant the foregoing general conclusion and the following brief statement. The qualities of the gentes which compose a cohort differ fortuitously in such a way as to form a continuous polygon of frequency. The cohorts, when treated statistically, also disclose a continuous relationship. When the socii themselves are assembled, they vary about an average condition in the same way that individual variants group themselves about a median condition. Let me recall the primary contention that it is here in the earlier stages of organic differentiation that

we must look for the true facts. If orthogenesis is real, it will be found here. But the evidence is all to the contrary. I am well aware that this may seem to be a very cavalier treatment of a large subject, but it is my purpose only to present the conclusions which are authorized and justified by the results of the present investigation. And this summary statement must suffice.

And now, by way of conclusion, I may outline what I believe to be the full and correct statement regarding the history of organic differentiation among the Partulae, as it has gone forward in the past and as it is proceeding to-day. The efficient causes of evolution are congenital, and their work is manifested by the continuance of some among the parental qualities; but these are never repeated faithfully, for the hereditary chromosomal machinery is such that exact similarity is impossible. The individual differences may be small or larger, but the degree is unimportant—it is congenital causation that is the essential element. The variants then exercise their hereditary endowments as they may, with success or failure as the outcome of their accord with the whole complex of surrounding circumstances. They must not be unadapted—this is the true biological categorical imperative. Nature makes a wide allowance in the matter of actual utilitarian values.

Variation and heredity, then, are the two aspects of the workings of the internal factorial machinery; natural selection, with which I include spatial and physiological isolation, does the rest. The whole complex of external conditions, whatever these may chance to be, does nothing in the way of originating variations; its effects are limited to an acceptance, a tolerance or a rejection of the varied aspirants for the career of a complete organic life.

HENRY E. CRAMPTON

BARNARD COLLEGE,
COLUMBIA UNIVERSITY

RESEARCH AND THE TRAINING OF THE RESEARCHER

I

RESEARCH is systematic and critical investigation into the sources of truth; it is a characteristic and proudly accepted function of the university. In the eyes of the world the university degree, the doctor's degree, stands for competency in scholarly pursuit of truth. In granting the degree the university acknowledges, tacitly at least, responsibility for *training in research* of potential researchers. Are the functions desirably to be differentiated?

(1) One policy, not uncommon, admits the candidate for the doctor's degree to a professorial undertaking in research. He may, at the discretion of the professor, take such part in the investigation as appears compatible with its validity and profit therefrom in "training" as he can. Responsibility, however, lies with the professor; the investigation is his investigation. Thus, properly, the candidate is follower and not director of inquiry; he pursues a technique chosen and directed by another; he is executor of a plan not his own. If he plays his part of technical assistant to the satisfaction of the professor, thereby, so far as research enters, he qualifies for the doctor's degree.

(2) A second policy does not admit the candidate to staff research; it assigns him to independent research. The candidate is not an assistant whom the professor may use at his discretion for the forwarding of his own researches; he is, rather, an initiate in self-directed inquiry, for whom the professor is a resource of advice and criticism. His independent research is both a medium for the development of research ability, and a test of that ability. By it he is judged to be competent or not competent in research.

(3) A third policy is intermediate. The policy admits the candidate to a part in execution of more than one professional inquiry, each designed, directed and controlled throughout by the responsible staff member. When the candidate by repeated practice under direction appears to have mastered the essentials of a variously flexible technique, he is released from his auxiliary status and assigned to independent research. Again by his independent work as researcher he manifests his competency or incompetency.

II

Now the end of research is truth discovered. To that end error, so far as is humanly possible, must be kept out of investigations. The obligation of the university in its research function is to maintain the highest quality of truth-seeking that the capacities of its membership and the extent of its material resources permit. Hence research must be directed and controlled by the select and the proven in research—namely, the experienced and competent staff membership.

(1) In the first policy described above, that principle is clearly accepted. There is no research other than staff research. The policy permits, if it does not ensure, the highest attainable quality in all research for which the university stands sponsor.

(2) The second policy segregates staff research from the research of candidates. The staff is in no wise hindered in the most effective use of its resources