GEOGRAPHICAL ISOLATION AND THE ORIGIN OF SPECIES.

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It is a fundamental principle of science that man has no answer to any problem until, through observation and experiment, he is able to find it out. He must work from individual details, an adequate number of which will enable him to frame a more or less complete generalization. Such result, however, is not necessarily final because every inductive solution reveals new problems. Other factors, not originally discerned, may confuse conclusions or a farther cause must in turn be explored.

For example, we have worked out in detail the proximate origin of tens of thousands of species of animals and plants, but we cannot minutely trace pedigrees through geologic ages. Here ancestral records are lost in the "infinite azure of the past," to be sought only by the torchlight of palaeontology. Furthermore we can rarely affirm one single cause or group of causes as covering the whole range of the phenomena studied.

In a recent address at Toronto, Professor WILLIAM BATESON asserted that as to the origin of species "we have no clear answer to give. Faith has given place to agnosticism." This remark and others in the same address have been widely quoted and as widely misunderstood as indicating a loss of confidence on the part of one of Evolution's ablest defenders. Yet BATESON continues: "Although our faith in Evolution stands unshaken, we have no acceptable account of the origin of species."

This expression is susceptible of two interpretations. It may have been a large and generous gesture, disclaiming for science any approach to omniscience. For even by science, the coordination of all human experience, we never arrive at any ultimate cause whatever; the laws we establish are merely the way we find things working, in DARWIN's words, "the observed sequence of events". Or the statement may have been merely a revelation of the speaker's ignorance of the researches of students of geographical distribution and of taxonomy generally. For in regard to the latter he observes: "They have built up a vast edifice of knowledge which they are willing to share with us and which we greatly need. The separation between the laboratory men and the systematists already imperils the work, I might say the sanity of both."

With all respect to the eminent English investigator, I am sure that he fails to do justice to geographic research in biology, confusing all investigations of fauna and flora with the special function of the systematist. Had he ever undertaken a serious study of species as they exist, ranging over the face of the earth, he would hardly have made the concession to nonscience to which I have briefly referred.

For the real problem at issue is that of the origin of each one of the millions of *individual* species. On this a prodigious array of facts have been gathered and important generalizations tentatively established. The very extent and multiplicity of our knowledge make it impossible to express in a single phrase what we know of the origin of species. It is true enough that natural selection, alone, does not satisfy as a complete answer. Nor can any other single word or phrase designate the whole range of modified divergence on which depends the origin of species.

In the study of any species whatever, we encounter four factors: two intrinsic — Heredity and

Variation; two extrinsic — Selection and Isolation [1]), — the one ensuring the non-survival of the non-adaptable, the other leading to mating by propinquity, through biological friction which prevents wide crossing by interrupting the fluidity of life. Factors other than these four may exist, but in the history of every individual of which a species is composed, each of these is potent. With that fact in mind, in view of the great range of investigation covering these matters, one may affirm that no wide-reaching biological problem is more completely explained than that of "the Origin of Species."

The word „species" itself needs perhaps re-definition. A species is a single "kind" or definable form in the natural divergence of animals and plants. In any case, the species found in nature are genuine species; nothing can be more real than that which exists in nature. Natural species, nevertheless, have as a rule indefinite boundaries shading off into subspecies, geminate or representative species, ontogenetic forms and the like, and may be variously altered by artificial selection in conjunction with artificial segregation. All their multifarious eccentricities command attention. As DARWIN once observed, such facts are fascinating to us "as speculatists, however odious to us as systematists". They must be reckoned with, not through speculation but by intimate understanding of evident realities. But to extend our knowledge of a species we must ring the changes on the variations to which it is susceptible. For the degree of variability is also a specific character. On such problems hundreds of geneticists are now at work, with the handicap that their studies look forward to changes that may be effected, not backward to ancient responses to shifting environment.

The historic origin of individual species of living organisms runs closely parallel with the origin of individual words in a language. One may trace the derivation of thousands of words, while yet hesitating about or "expressing agnosticism" as to the origin of language. In like fashion, we may trace back to their original stocks thousands of animal or plant species and still hesitate about or "express agnosticism" as to a complete definition of biological origins. For after all each one has its own history, including vicissitudes of migration, selection, and separation; and the theoretical generalization can be only an inductive summing up of all evidence obtained.

In the study of species as related to geographical conditions, one is most impressed by the recognition of "twin" species, forms closely related but nevertheless distinct, separated from each other by some kind of barrier. To similar parallel forms I gave in 1908 the name of "geminate species". These agree with each other in generic structural traits. In all matters of adaptation to environment, presumably results of selection, they may be absolutely identical, as also in habits unless confronted by some novel condition. They differ in minor regards, presumably of later origin than the generic traits.

I indicated the law of geminate species as follows:

Given any species, in any region, the nearest related species is not to be found in the same region nor in any remote region, but in a neighboring district separated from the first by a barrier of some sort or at least by a belt of country the breadth of which gives the effect of a barrier.

The ornithologist, Dr. JOEL A. ALLEN, accepted the above generalization and called it "Jordan's Law", but it of course rests on the observation of many workers. For it is a matter of common knowledge among field naturalists that the minor differences which separate species and subspecies are due to some form of segregation or isolation. Selection produces adaptation, but the distinctive characters of species are in general non-adaptive. By some barrier or other the members of one minor group are prevented from interbreeding with those of another minor group or with the mass of the species. As a result, local peculiarities are fixed. "Migration holds species true, localization lets them slip," or rather leaves them in the backwash of currents of Evolution. Peculiarities thus set off by isolation become intensified by in-and-in breeding, and the particular environment exercises some continuous type of selection until at last there emerges a new form, recognizable as distinct. And while its range rarely coincides with that of the parent species, or with any other closely cognate form, neither is it likely to be located far away. In the few cases where the range of geminate species overlaps in any degree, the fact seems to find an explanation in the surmounting (to some extent) of

1) Isolation, separation, segregation, are different expressions for the same phenomena — the conception perhaps best expressed by the German phrase, *"räumliche Sonderung"*.

a barrier by one or other of the twin forms. The obvious immediate element in the formation and molding of species is therefore isolation, with (behind) the factors of heredity, variation, selection, and others as yet more or less hypothetical.

Illustrations of geminate species of birds, mammals, fishes, reptiles, snails, and insects, are well known to all students of these groups; examples may be found on every hand. I have myself gathered the record of hundreds of pairs of zoological twins, an enumeration for which the present paper has no space [1]).

It is clear enough that species change with space and with time. With space, because separation takes place and new environment brings new stress of selection while isolation of individuals involves some difference in parentage. In like fashion, species change with time, because new conditions arise, new enemies, new foods, new separations, new selections. That notable differences obtain in time, even in pure strains, and when there is no visible reason for change, is clearly shown by the experience of stock-breeders. In geologic time one geminate species often follows another and in the same locality, a fact lately shown by the writer in an extensive survey of the Miocene fish fauna of California [2]).

The application of Jordan's Law to plants has been denied. But geminate species are just as prevalent in botany as in zoology, and the effects of isolation in species-forming among plants are just as distinct. They are merely obscured by special conditions which obtain among plants.

Crossing the temperate zone anywhere on east and west lines, we find plant after plant replaced across barriers by closely related forms. Illustrations may be taken anywhere from among the higher types-equally well, no doubt, from among lower ones. Some genera belt the earth or come very near doing so, each form having its twin as next neighbor. A single example, that of the plane tree, *Platanus*, may suffice.

A natural law is not invalidated by the presence of effects due to other causes in the same environment. Actual conditions in nature are everywhere products not of single and simple forces, but resultants of many causative influences, often operative through the long course of ages.

As a rule, related species in almost every group are connected by a fringe of intergradations or subspecies. Where barriers are sharply defined, geminate species also are sharply defined. Where diffuse, geographical subspecies connect them, either wholly or in part. We recognize no difference between species and subspecies except that involved in sharpness of definition. If the particular barrier cannot now be crossed, a species resultant from the barrier will be well defined and therefore unquestionable, however small the elements of difference. Subspecies are commonly associated with some feature of geographical distribution.

It has been claimed that geminate forms are not true species because they often intergrade one with another, and would probably be lost by intermingling were the barriers removed. Some maintain also that only physiological tests can be trusted, as true species will not blend and their hybrids if they exist, are sterile. This assumption is purely hypothetical. Interbreeding is no test of species. Closely related species in almost any group of plants or animals can usually be readily crossed. As the relation becomes less intimate, we find partial sterility of varying grades or even total incompatibility.

In most groups, probably in all, the characters which distinguish species from one another are elements neither useful nor injurious. Unless we take "Natural Selection" to cover both processes, as DARWIN certainly did, we must assign to "selection" the preservation and intensification of adaptive characters, and to "isolation" the seizing and fixing of the non-useful — usually fluctuating — element. It is a fact well know to breeders that these indifferent or non-useful characters are generally more persistent in heredity than traits which are plainly adaptive. The slight traits which mark races are in themselves not obviously valuable in the struggle for existence.

MORITZ WAGNER, the pioneer in this line of investigation, showed plainly that in the study of the evolution of any form we need to know where it has lived, what it did, how it was bounded,

1) See Dudley Memorial Volume, Stanford University Press, 1913.
2) Fossil Fishes of the California Tertiary: Stanford University Press, 1921.

and what was its relation to other forms, geographically as well as morphologically. His work, a most necessary supplement to that of DARWIN, has never received the attention it deserves. This is due in part to the fact that most investigators do not travel. They know little of animal or plant geography at first hand. They have had nothing to do with species as living, varying, reproducing, adapting, and spreading groups of organisms. Another reason lies in WAGNER's attitude of opposition to Darwinism. For Natural Selection he substituted Separation, *"räumliche Sonderung"*, denying altogether the potency of the former factor. He saw the two as competing, not cooperating elements, and thus threw on isolation the impossible task of accounting for adaptation. One need not ascribe to Natural Selection the *"Allmacht"* which some Neo-Darwinians have claimed for it, yet on the other hand those who reject it as a factor in organic evolution give no rational explanation of the universality of adaptive organs and adaptive traits, no clue to the most universal characters of organisms in general.

Certain writers urge that neither selection nor isolation are factors in evolution, but rather elements in species-forming, a process defined as something distinct from evolution. They say that these obstacles in the stream of life only help to split on-moving groups of organisms into different categories, while the impulse to forward movement is internal and the changes of evolution proper affect groups as a whole, and are not concerned with dividing them into species.

Such a view may be questioned on two grounds; it is untrue as to facts, or else merely a matter of words. We know nothing of evolution *in vacuo*, of change in life unrelated to environment. All forms of life are split up into species, with adaptation to external conditions visible in every structure. We know of no way in which organisms become adapted to special conditions except by the progressive failures of those which do not fit. No organism has escaped or can escape the grasp of selection. In like manner, the world being full of physical barriers, no organism escapes the biological friction which prevents uniformity in breeding. There must be some degree of *"räumliche Sonderung"*, even in a drop of water.

To admit these facts and yet say that selection and isolation are not factors in evolution would appear to make the matter a mere question of words. If by evolution we mean the theoretical progress of life, due solely to forces intrinsic in organisms, then outside influences are of course not factors in such evolution. If, however, we mean the actual life movements of actual organisms on this actual earth, then extrinsic influences and obstacles are factors in continuous, diverging change.