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EACH AFTER HIS KIND[1]

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HAVING chosen a biblical title for my talk this evening, I may well conform to classical, and clerical, precedent by following it with an appropriate text. My text, then, is taken from the first and second chapters of the Book of Genesis.

And God said, Let the earth bring forth grass, the herb yielding seed, and the fruit tree yielding fruit after his kind, whose seed is in itself, upon the earth: and it was so.

And God created great whales, and every living creature that moveth, which the waters brought forth abundantly, after their kind, and every winged fowl after his kind: and God saw that it was good.

And out of the ground the Lord God formed every beast of the field, and every fowl of the air; and brought them unto Adam to see what he would call them: and whatsoever Adam called every living creature, that was the name thereof.

And Adam gave names to all cattle, and to the fowl of the air, and to every beast of the field; . . .

Thus we see that the science, or at any rate the art, of nomenclature had a simple and auspicious beginning. Not only was Adam assured on the highest authority that "every beast of the field, and every fowl of the air" would continue to reproduce with fidelity "after his kind," but that whatever names he should give to them would stick—a boon that would be greatly appreciated by present-day taxonomists. Verily, the Garden of Eden at that time was a nomenclator's paradise, for every species was a new one and there was no need to search through dusty tomes for

[1] Address of the retiring vice-president and chairman of the Section for the Zoological Sciences of the American Association for the Advancement of Science, Philadelphia, December 31, 1940.

possible antedating descriptions, in order to establish a list of synonymy. Moreover, there was no one, not even Eve, to question the appropriateness of the names chosen or whether they conformed to the latest international rules. Indeed, there is reason to suspect that most of them were *nomina nuda;* and there is no basis for believing that they followed the binomial system—which is perhaps just as well, for it is trouble enough to check synonymies back to the *Species Plantarum* and the tenth edition of the *Systema Naturae.*

There is little evidence that Adam gave much thought to taxonomy. In this I think he may well be excused, for he must have been kept pretty busy with such a host of animals and plants to name and have had little leisure for the contemplation of comparative morphology and its implications. Nevertheless, the system he inaugurated apparently served the needs of man fairly well for a good many centuries. Of course it was scarcely to be expected that everything would go along so smoothly indefinitely, especially after the advent of Eve and the unfortunate episode of the apple. In fact Adam's nomenclatorial troubles may have started soon thereafter. I confess the account comes from an apocryphal source—perhaps it was one of John Kendrick Bangs's amusing phantasies—but I recall reading somewhere years ago of Eve's assistance in naming some of the animals. Apparently the job was too big for Adam alone; it dragged along and was still unfinished when Eve arrived on the scene. She naturally wanted to participate in the fun. So Adam assigned to her some of the animals to name while he was out rounding up a bunch of new species for the next day's work. In checking with her that evening Adam noticed one large beast different from anything they had encountered before and he was curious to know what Eve had named it. Inquiry elicited the information that she had called it an *elephant.* "But," asked Adam, "why elephant?" "Because," Eve replied, with the prototype of true feminine logic, "it looks like an elephant." That was that, and no further argument developed—it has been an elephant ever since.

By this time, you have perhaps begun to suspect that I plan to discuss some phases of nomenclature and the problems that arise in taxonomy and systematics. When I mentioned this intention to some of my colleagues their looks seemed to say as clearly as words, "What do you know about taxonomy in the first place? And besides, everything has been said on the subject that can be said anyway." To the first, I can only reply meekly that I once ventured to describe a few species in an amateurish way; and as for the second, I had already sent in my title before I had seen "The New Systematics," the latest, if not the last, word on the subject (in 853 pages!)—and it was then too late to retreat. Still, I am not sure that I should have wanted to back out if I could, as I have had this subject on my mind for years. The impulse to say something on it perhaps stems back to my student days. Where our graduate group worked there was an iron grill which separated the museum from the zoological laboratories. It separated almost as effectually the "species splitters" on the one side from the "sperm chasers" on the other—or, presumably, the ovine from the caprine biologists; but there was complete lack of agreement as to how this classification should be applied. It is true, there were a few who knew the combination on the wicket gate separating the two provinces and who occasionally passed through; and it was my good fortune to be one who was at least tolerated on both sides.

The situation as I have described it in those far-off student days is not greatly exaggerated and was indicative of an all too general attitude among zoologists. The field naturalist and museum worker felt that the "closet zoologist," as he dubbed the laboratory investigator, was working under such artificial conditions that his findings had little relation to animals in "natural" surroundings. Above all, that he had little conception of taxonomic problems, and the chances were that if he should meet in the wild the animal on whose tissues he was working he would not recognize it. The embryologist, physiologist or cytologist on his part accused the taxonomist of playing a game about on a par with arranging a collection of postage stamps, and of splitting genera into species, and species into subspecies, merely for the doubtful distinction of getting his name attached to the specimens and embalmed for posterity and for eternity along with them. The new science of genetics was just getting started and with the bumptious confidence of youth was maintaining that the analysis of the genetic factors would soon settle the question of taxonomic species for once and all; while a short time previously the equally enthusiastic devotees of bio-statistics were offering to do the same thing by mathematical formulae. None of these proposals was embraced by the taxonomists with enthusiasm nor did they tend to draw the two camps closer together. Nevertheless, as the years have passed both sides have come more and more to see that they are dealing with different aspects of the same questions; biologists generally are coming to recognize that what an animal or plant is or can be in its physiological or morphological, or even teratological, responses—whether in its natural surroundings, in the laboratory, the garden plot or under domestication—is all an expression of its innate capacities and as such should be taken into account. The only reason the extreme responses are not ordinarily encountered "in nature" is that the natural environment does not com-

monly reproduce the extreme or unusual conditions of the laboratory.

The primary purpose of giving names, of course, is to furnish "handles" by which animals or plants may be identified and designated in reference. A breeder of cattle may give a distinguishing name to every animal in his herd and an experimenter with the larger animals, and to some extent with plants, may distinguish each individual with which he deals by a separate designation. Obviously this is not feasible for the whole array of organisms in nature, or even those which are selected for descriptive study and preservation in collections. Nor would it serve any useful purpose if it could be done. Hence some sort of grouping must be made, and the names applied to the collective groups. The most natural and generally useful grouping is to put together forms having certain morphological or qualitative characteristics in common, although of course many other groupings are possible, such as those based on geographical or ecological habitat, and the like. As Coulter has put it, nature makes individuals, and man makes species.

Neither sacred nor apocryphal history informs us whether there was more than one kind of elephant represented in the Eden Zoo; but we are told that each was to reproduce "after his kind," which introduces the factor of genetic relationship. Even without this element, further classification than that into independent "kinds" is possible, just as it is of inanimate objects. There are, moreover, different degrees of resemblance, from which a hierarchic system of grouping results, irrespective of any necessary genetic relationship. The beginning of systematics is, then, the classification of organisms according to their degree of similarity, though in this there is room for disagreement as to the relative value of different characters in determining similarity. To take a crude but not a fanciful example, whales once were classed as fishes because they both swim in the sea. Such questions are sublimated to much greater refinement to-day, but they still cause a large share of the instability and contentions of taxonomy. Possibly this is another penalty of Eve's consuming pomological curiosity.

Community of descent gives a basis of classification of another sort. Until fairly recent times it was generally taken for granted that each kind, or species, of organism was descended unchanged, except for a certain amount of intraspecific variation, directly from its original creation. But as more extensive collections were made intermediates became more and more troublesome and it became increasingly difficult to define the limits of the species, in spite of help given by certain pious naturalists. One American conchologist, for example, was reported as dropping such unregenerate specimens on the floor and stepping on them, explaining that they were anomalous perversions the Creator never intended anyway; and it is rumored that at least one botanist aided divine intention in a similar manner. It will be recalled that the elder Agassiz held to the thesis that species were individually created according to a divine plan, even after the idea of evolution had become adopted by the generality of biologists. With the acceptance of evolution the systematist strove to make his classifications as "natural" as possible; he not only wanted his arrangements to show the morphological resemblances between groups, but he tried to select those characters for his purpose that would bring together the groups most closely related in actual genetic descent. His goal was not only a *system* but actually a genealogical chart. But except in a few recent instances the process of species making has not been actually observed. As a consequence the course of descent has had to be inferred from morphological, embryological and other evidence, and hence is open to different interpretations and to frequent change as more facts are accumulated. In fact, systematics plays a double role, *viz.*, the defining, describing and naming of groups, with the inference that in arranging them their descent, and hence their genetic relationship, is being portrayed at the same time. This duality of modern taxonomy has often been pointed out and the proposal to divorce *naming* completely from any implications as to *relationship* has been suggested by a number of authors as a panacea for nomenclatorial ills.

ARE SPECIES A REALITY?

Systematists generally look upon the species as being the most real, and in that sense the most important, basic biological group. The groupings above the species are assumed to differ not only in rank but in kind from those below it. Still there is much disagreement as to whether there is really any such definite entity as a species, and although numberless attempts have been made to define it, and tomes have been written on the subject, no universally acceptable definition has yet been forthcoming. Earlier definitions were based primarily on resemblance, while later ones tend to emphasize the dynamic nature of the species concept. Dobzhansky, for example, has recently characterized a species as "that stage of evolutionary process, at which the once actually or potentially interbreeding array of forms becomes segregated into two or more separate arrays which are physiologically incapable of interbreeding,"[2] and adds that the "species is a stage in a process, not a static unit." The older definitions use the criteria of resemblances and assume that classification by them will give a fair picture of genetic relationship; the other tests relationship by breeding

[2] "Genetics and the Origin of Species," 1937, p. 312.

behavior and assumes that greater resemblance should ensue from closer genetic similarity, as indicated by the capability of interbreeding. Even Darwin avoided defining a species, but said: "No one definition has satisfied all naturalists, yet every naturalist knows vaguely what he means when he speaks of a species." Arthur searched the "Origin of Species" for a more definite statement and reported as follows:[3] "If a man were going to revolutionize the world of thought he certainly, I assumed, would give a definition of the subject he is going to treat. But I could not find a word as to what Darwin meant by a species. Yet I did find this in the latter part of the last chapter; he says, 'And now we shall be freed from the vain search for the undiscovered and undiscoverable essence of the term species.'" "Consequently," Arthur concludes, "here we are, tracing a will-o'-the-wisp."

From the pre-Darwinian view of the definiteness, fixity and separate origin of species, opinions of many swung to the completely opposite extreme. Bessey, for example, asserted that "species have no actual existence in nature. They are mental concepts, and nothing more."[4] East probably represented general opinion more accurately when he said,[5] "In a sense, a species is a human concept and as such its definition may be carried to any ridiculous extreme, yet there is no more striking biological fact than that *in general* the great groups of living things do fall into specific subdivisions which many criteria show to be distinct, discontinuous, without intermediates." That such definite, distinct groups may in certain cases arise suddenly and completely at a single jump is evidenced by the few authentically known cases of amphidiploidy; but this can not be the general, and certainly not the universal, mode of species formation.

The mammalogists and ornithologists in this country have devoted special attention to taxonomic procedure and brought it to a relatively high state of perfection. This is probably due in part to the fact that these groups are relatively homogeneous and much more completely known than most others. The concept of species developed by Allen, Merriam and others of that time has recently been modernized a bit and is stated by Mayr as follows:[6] "A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or hybridize wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers." Be it noted that in practice, in the absence of controlled experimentation, the ability to hybridize (I prefer the word interbreed in this connection) must be inferred from the observable intergradation. Let us take a case in point familiar to most of us. Our common bob-white quail varies from a large, pale bird in New England to a small dark form in the humid region of southern Florida. Chapman says:[7] "No one who compared this small, dark Florida Quail with the large, pale Quail of New England would consider them the same species. But on examining a series of Quails from all the Atlantic States one sees how gradually this change in color and decrease in size occurs, and that nowhere would it be possible to draw a line separating the two extremes." The Florida form is, therefore, accounted but a subspecies of *Colinus virginianus,* which view is further substantiated by the fact that the two are highly, if not completely interfertile. "But," adds Chapman, "if through any change in the earth's surface the regions occupied by the large, light Quail and the small, dark one should be separated, the intermediates would disappear and instead of a race or subspecies we would have a full species—*Colinus floridanus.*" This would not be the case, however, with Mayr's definition, since the two extremes would presumably be "potentially capable" of interbreeding even should the intermediates disappear. Here again we encounter the conflict between the purely descriptive criterion and the attempt to include genetic relationship. The situation is still more anomalous in those cases, by no means rare, in which the series of intergrading subspecies returns on itself, forming a ring or *Rassenkreis,* the remote members of which may come to occupy the same territory. Dice has described such a case in a species of deer mouse, *Peromyscus maniculatus.*[8] In Michigan are found two subspecies, *bairdii* and *gracilis,* living side-by-side, but occupying generally different ecological habitats, and showing no evidence of intergradation. They are considered subspecies rather than full species, because "*gracilis* is said to intergrade westerly with *borealis* which in turn intergrades with *osgoodi, osgoodi* with *nebrascensis,* and *nebrascensis* with *bairdii,*" thus closing the ring. Cases of this sort invalidate the supposed law, long held to be of general application, that while two closely related species might overlap in the same locality, two subspecies of the same species could not do so. This would undoubtedly be the case were there not some barrier to natural interbreeding, for there would otherwise be mixture and intergradation. In this case the different ecological habitats may be the barrier that keeps them apart, although it is perhaps not the only factor. At any rate, Dice has shown that

[3] *Amer. Nat.,* 42: 244, 1908.
[4] *Ibid.,* 42: 218, 1908.
[5] *Ibid.,* 54: 262, 1920.
[6] *Ibid.,* 74: 256, 1940.
[7] "Handbook of Birds of Eastern North America," 1895, p. 4.
[8] *Jour. Mammal.,* 12: 210–213, 1931.

the two forms may be interbred in the laboratory and fertile young produced.

In contrast to such complexes within species, in which the subspecies may be differentiated by morphological distinctions, are others consisting of groups showing only slight morphological differences but with as much intersterility as ordinarily distinguishes full species. An important example is that of the malaria mosquito, *Anopheles maculipennis*. It was early noticed that malaria might be widespread in certain localities and rare in others, though this mosquito was equally common in both. Subsequently it was found that while the adults were practically indistinguishable, at least six "races" could be established on well-defined characters of the eggs. These races differ in ecological habitat and in the habits of the adult, which in turn are correlated with their importance as vectors of malaria. The race, or subspecies, *typicus* does not feed on man if other sources of food are available and hence is of little importance as a malaria carrier. Another, *atroparvus*, "is occasionally a source of mild endemic malaria"; *labranchiae* is "a dangerous malaria carrier"; and *elutus* "is always associated with intense malaria."[9] It early appeared probable that these forms remained constant even when present in the same area; and later intensive breeding experiments revealed within what would appear to be a fairly uniform species as based on morphological characters, the same degrees of sterility commonly encountered between well-recognized species, or even genera, in other groups of animals as well as in plants. Turrill remarks of the latter that:[10] "Species widely different morphologically may be fertile one with another and yield fertile offspring, as in many orchids, while species differing in few obvious characters may be inter-sterile, as in some buttercups."

Rassenkreise, or "clines" as Huxley designates them, are due primarily to a differential distribution of genes through an interbreeding population. Such a situation may be produced by any factors, geographic, ecologic or genetic, which interfere with complete random mating, thus leading to some degree of inbreeding and the formation of local populations differing in gene frequency if not in actual genes. The theoretical effects of the interaction of breeding barriers, selection and mutation rate, which have been worked out, particularly by Wright, need not be gone into here. The groups formed in this way are the taxonomist's subspecies or races and the question we are concerned with at the moment is, how and when may they become *bona fide* species? On the basis of descriptive characters, we may say at the level where there is a definite gap between one group and others most similar to it; considering it genetically, *i.e.*, dynamically, we would say with Dobzhansky, when it is physiologically incapable of interbreeding with closely related groups. But we have already seen that neither of these is practically applicable in all cases.

One thing is clearly apparent, namely, that differentiation within a population may result from any cause, whatever its nature—genetic or otherwise—which interferes with the free and unrestricted distribution of the genes among its component members. Sterility, far from being due to a single cause, may result from many causes. There is not time for a full discussion of sterility, but some of the factors which may interfere with free interbreeding, or which tend to produce a differential in favor of some matings over others, may be listed:

Geographic—islands, mountain ranges, rivers, etc. Mere distance, bringing certain members of the population into closer propinquity to some of their neighbors than others farther away.

Ecologic—Physiographic and biotic habitats; temperature, moisture, altitude, etc.

Morphologic—Size; structure of parts, particularly of genitalia.

Physiologic—Age and time of sexual maturity, health, longevity, physiology of reproduction, reactions to stimuli. (I have elsewhere made the suggestion that length of day acting on differently attuned biotypes may be a factor in effecting a rough stratification of breeding mourning dove populations with reference to latitude, thus tending to some degree of inbreeding.)[11]

Genetic—Gene mutation; chromosome aberrations, including inversions, deficiencies, translocations, segmental interchange and polyploidy.

Psychologic—Sex recognition; courtship and mating behavior; pugnacity.

One or more of these causes may be primarily operative in certain cases of differentiation, or any combination of them. Complete breeding isolation may occasionally be brought about in a single jump, such as amphidiploidy, previously mentioned. Possibly also a single mutation which profoundly affects developmental rates and so induces profound modifications, as suggested by Goldschmidt,[12] may have a like effect. It would seem, however, that more usually speciation is a gradual process, and Muller[13] maintains that cumulative gene mutations alone may suffice to bring about interspecific incompatibility. In view of all this multiplicity of causes it becomes obvious why species are so difficult to define.

(*To be concluded*)

[9] "The New Systematics," 1940, p. 353.
[10] *Ibid.*, 1940, p. 65.
[11] *Auk*, 50: 284–296, 1933.
[12] SCIENCE, 78: 539–547, 1933.
[13] "The New Systematics," 1940, pp. 186–268.