EVOLUTION and the DIVERSITY of LIFE

SELECTED ESSAYS

ERNST MAYR

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The Biological Meaning of Species

There is perhaps no other subject in biology for which one can document as long-standing a controversy as the species concept. If one gathered together all that has ever been written about the species, it would easily fill several shelves in a library. What then is the reason for so much confusion?

There are actually many reasons, but it would not be worthwhile to pursue them all. Many of the difficulties have been removed in recent years. Let me start with a most elementary linguistic consideration. It is necessary to make a distinction between categories and taxa. The concept *tree* is a category, but actual trees such as willows, oaks, and pines are taxa that we place in the category tree. The categories employed by the taxonomist are species, genus, family, order, and so forth, but the words robin, blackbird, chiff-chaff, and blue tit signify taxa to be placed in the species category. We see here at once that there are two levels of difficulties, the delimitation of taxa and their ranking in the proper category.

Let me illustrate this with a human example. There was a widespread theory in the early nineteenth century that the human races had descended from the different sons of Noah and were actually different species. On the taxon level, this posed the problem whether an intermediate population, let us say the North Africans, should be placed in the taxon of the Caucasians or that of the Negroes. This, then, was one species problem. The second problem was whether the proper category for each of these human types was that of the species or the subspecies. This second decision depends entirely on the concept of species adopted, whereas the placing of the North Africans with either the white or the Negro race has nothing to do with the species concept as such. Much of the argument about the species concept has been due to the confusion between these two classes of problems, those having to do with the assignment of populations to taxa and those having to do with the ranking of these taxa in categories. This will all become clearer as we go more deeply into the arguments.

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Let us start with a historical survey of different species concepts. Considering the reams of paper devoted to the subject, it comes as somewhat of a surprise to learn that all the countless species definitions can be assigned to no more than three basic concepts of the category of the species.

THE TYPOLOGICAL OR ESSENTIALIST SPECIES CONCEPT

According to the typological concept, the observed diversity of the universe reflects the existence of a limited number of underlying "universals," or types. Individuals do not stand in any special relation to each other, being merely expressions of the same type. Variation is the result of imperfect manifestations of the idea implicit in each species. This species concept, going back to the philosophies of Plato (his *eidos*) and Aristotle, was the species concept of Linnaeus and his followers. This school of philosophy is now usually referred to as *essentialism*, following Karl Popper, and its species concept as the essentialist species concept. According to it, species can be recognized by their essential natures or essential characters, and these are expressed in their morphology. In its practical application, this species concept is usually called the morphological species concept.

In retrospect, it becomes obvious that not even Linnaeus and his followers had a strictly morphological species concept. For instance, Linnaeus described the male and the female mallard duck as two different species. When it was realized that the two so-called species were nothing but male and female, they were without hesitation combined into a single species even though there had been no change in the degree of morphological difference.

Even though morphological evidence is still used as a basis for inferences on the delimitations of biological species, a morphological species concept is no longer maintained by the modern biologist. In addition to the various conceptual reasons for its rejection are two practical ones. First, individuals are frequently found in nature that are clearly conspecific with other individuals in spite of striking morphological differences owing to sexual dimorphism, age differences, polymorphism and other forms of individual variation. An essentialist species concept is helpless in the face of caterpillar and butterfly, or sporophyte and gametophyte among plants, or whatever other drastic forms of intraspecific variation are found in nature. It is equally helpless in the face of so-called sibling species, that is, perfectly good genetic species which lack conspicuous morphological differences. Its theoretical as well as its practical weaknesses are the reasons why the essentialist species concept is now universally abandoned.

THE NOMINALISTIC SPECIES CONCEPT

The nominalists (Occam and his followers) deny the existence of "real" universals. For them only individuals exist, while species are

manmade constructs. The nominalistic species concept was popular in France in the eighteenth century and has some adherents to the present day, particularly among botanists. Bessey (1908) expressed this viewpoint particularly well: "Nature produces individuals and nothing more. . . . Species have no actual existence in nature. They are mental concepts and nothing more. . . . Species have been invented in order that we may refer to great numbers of individuals collectively."

When I read statements such as this, I always remember an experience I had 40 years ago when I lived all alone with a primitive tribe of Papuans in the mountains of New Guinea. These superb woodsmen had 136 names for the 137 species of birds I distinguished (confusing only two nondescript species of warblers). That primitive Stone Age man recognizes the same entities of nature as western university-trained scientists refutes rather decisively the claim that species are nothing but a product of human imagination. The same, of course, is true for the sharp definition of animal species in our neighborhood. When you study the birds in your woods and gardens, do you ever find intermediates between blue tits and great tits, or between thrushes and blackbirds, or between jackdaws and rooks? Of course you do not. Every species of bird, mammal, or other higher animal is extraordinarily well defined at a given locality, and hybridization or intermediacy is a rare exception. Species are the product of evolution and not of the human mind. However, the nominalist species concept may well be legitimate when one deals with inanimate objects and particularly with human artifacts. It ignores, however, the fact that there is a fundamental difference between classes of *objects* that are the product of the human mind, like kinds of furniture, and classes of *organisms* that are the product of evolution rather than of human imagination. As Simpson has emphasized correctly, the basic fallacy of the nominalists is their misinterpretation of the causal relation between similarity and relationship. Members of a species taxon are similar to each other because they share a common heritage. It is not true that they belong to this taxon because they are similar, as is claimed by the nominalists. The situation is the same as with identical twins. Two brothers are identical twins not because they are so extraordinarily similar, but they are so similar because they are both derived from a single zygote, that is, because they are identical twins. Incidentally, it is this same misinterpretation of the connection between similarity and relationship that is the fatal weakness of numerical phenetics. Anyone who believes in evolution must reject the nominalistic species concept.

THE BIOLOGICAL SPECIES CONCEPT

It began to be realized in the late eighteenth century that neither of these two medieval species concepts, the essentialistic and the nominalistic, was applicable to biological species. An entirely new species concept began to emerge after about 1750, but it took another 150 years before it had been thought through in all of its consequences. This third concept differs quite drastically from the concept of inanimate species. It rejects the idea of defining the species typologically as a "class of objects." Indeed, it breaks with all philosophical traditions by defining species purely biologically, as follows: *Species are groups of interbreeding natural populations that are reproductively isolated from other such groups.*

A species, owing to the properties mentioned in this definition, has three separate functions. First, it forms *a reproductive community.* The individuals of a species of animals (the situation is somewhat different in plants) recognize each other as potential mates and seek each other for the purpose of reproduction. The species-specific genetic program of every individual ensures intraspecific reproduction. Second, the species is also *an ecological unit* that, regardless of the individuals composing it, interacts as a unit with other species with which it shares the environment. The species, finally, is *a genetic unit* consisting of a large intercommunicating gene pool, whereas the individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time. In all three characteristics the biological species is nonarbitrarily defined, and differs quite drastically from so-called species of inanimate objects. It is called "biological" not because it deals with biological taxa, but because the definition is biological. It utilizes criteria that are meaningless as far as the inanimate world is concerned.

The species has two properties that distinguish it completely from all other taxonomic categories, let us say the genus. First of all, it permits a nonarbitrary definition—one might even go so far as to call it a self-operational definition—by stressing that it is defined by the noninterbreeding with other populations. Second, while all other categories are intrinsically defined, by having certain visible attributes, species are relationally defined. The word *species* corresponds very closely to other relational terms such as, for instance, the word *brother.* A given person is not a brother on the basis of certain intrinsic properties of his, but only in relation to someone else. A population is a species only with respect to other populations. To be a different species is not a matter of degree of difference but of relational distinctness.

The relational definition of the species is both the strength and the weakness of the biological species concept. It permits nonarbitrary decisions with respect to all other coexisting populations, that is, synchronic and sympatric species populations. This is where the concept is needed most frequently by the biologist and where its application faces the fewest difficulties. This is the situation sometimes referred to as the nondimensional species. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other, but the more irrelevant biologically this also becomes.

Before entering into a discussion of the biological significance of species, let me say a few words on the dimensions of this universe. Few nontaxonomists have any conception of the magnitude of biological diversity. More than a million species of animals have already been described and nearly half a million species of plants. However, our knowledge is highly uneven. Only about 3 new species of birds are described annually, a very small addition to the 8600 species previously recorded. But let us look at some other groups. I still remember the days when many papers were published in the genetic literature giving the name of the organism simply as *Drosophila.* This was implicitly considered to be synonymous with *D. melanogaster.* Now more than 1000 species of *Drosophila* are recognized, and almost as many new species were discovered in the last 17 years as in the 170 years preceding 1950. I want to give you another statistic. One group of mites, the chiggers (Trombiculidae), are now known to be of great medical importance as vectors of scrub-typhus and other rickettsial diseases. Only three species were known in 1900, 33 in 1912, 517 in 1952, and about 2250 in 1966. It is estimated that several hundred thousand species of mites in the many different families of this order still await description. What the total of species of animals is no one knows. It may be 3 million, it may be 5 million, and it may even be 10 million. Most taxonomists nowadays partition their time, devoting part of it to the more classical operations of taxonomy, the describing and classifying of species, and the other part to a study of the biological aspects of species. For nothing could be more discouraging than devoting one's life entirely to the endless collecting, describing, and naming of new species. To do only that would be nothing but stamp collecting. Describing does not make a scientist; a scientist wants to understand and explain. He wants to determine the causes of the multitude of phenomena and relations at the species level.

What are the kinds of question for which we look for a causal answer? Let me single out six major problems.

Discontinuity

"Why is variation in nature organized in the form of species rather than being continuous?" To be very frank, we have a descriptive answer to this question, perhaps I should say an empirical answer, but the complete causal analysis has only begun. To make clear what we are after, let us imagine a universe without species. Every individual in such a world may, during reproduction, exchange genetic material with any other individual. What would happen under this set of rules of the game? Every once in a while mutation and recombination would produce an individual that would be particularly successful in utilizing the resources of the environment. Alas, during the next reproductive period, this unique combination of genetic factors would be broken up and its genotype lost forever.

There are two ways of preventing this and nature has adopted both. One is to abandon sexual reproduction and maintain the superior genotype through asexual reproduction as long as the environmental situation lasts for which this genotype is specially adapted. The other solution, of course, is the "invention" of the species, if I may express myself that way, that is, the acquisition of a genetic program which will permit reproduction and genetic recombination only with such other individuals as are genetically similar, that is, conspecific.

The division of the total genetic variability of nature into discrete packages, the so-called species, that are separated from each other by reproductive barriers, prevents the production of too great a number of disharmonious, incompatible gene combinations. This is the basic biological meaning of species, and this is the reason why there are discontinuities between sympatric species. We do know that genotypes are extremely complex epigenetic systems. There are severe limits to the amount of genetic variability that can be accommodated in a single gene pool without producing too many incompatible gene combinations. We still do not understand why, on the whole, hybrids are not only far more frequent but also apparently less handicapped in plants than in animals.

The mechanisms that guarantee the discreteness of species are called the *isolating mechanisms*. There is a great diversity of such mechanisms, the sterility barrier being only one, and as far as animals are concerned, one of the less essential ones. Behavioral barriers are the most important class of isolating mechanisms in animals. It is necessary to emphasize that it is coded in the genetic program of every species to what signals an individual should respond during the reproductive period. The study of isolating mechanisms has become one of the most important and fascinating areas of biology, and every textbook of evolutionary biology, cytology, genetics, or behavior now deals with them quite extensively.

Multiplication of Species

The second great problem of species is that stated in the title of Darwin's great book *The Origin of Species*. How do species multiply? The answer to this question can now be stated in much more meaningful terms than was possible a generation ago. Species originate when populations acquire isolating mechanisms. A few special cases excepted, species multiply either by polyploidy (a process largely restricted to the plant kingdom) or by geographic speciation, that is by the genetic reconstruction of spatially isolated gene pools. The subject having been dealt with exhaustively in several recent books, I will say nothing further about it.

However, I would like to mention three sets of unsolved problems of speciation.

1. How frequent are exceptional situations, such as the sympatric evolution of host races into full species or the essentially sympatric origin of species through disruptive selection?

2. What role does chromosomal reorganization play during speciation? And how often does the acquisition of isolating mechanisms occur purely through genic mutation without any additional chromosomal reorganization?

3. To what extent does the acquisition of genic isolating mechanisms entail a reorganization of the entire epigenetic system?

Some of these questions may seem peculiar to someone who has not followed the recent genetic literature. However, unless I am very much mistaken I am discerning at the present time the emergence of a new area in genetics that constitutes a third set of problems related to the biological meaning of species.

The Genetics of Species

In the 1920s when I was a student and when the battle between the mutationists and the biometricians had not yet completely died down, there was a widespread idea that Mendelian factors controlled only the variation of intraspecific characters and that species differences were controlled by genetic factors in the cytoplasm. This idea has, of course, been dead for 40 years and even the discovery of DNA in mitochondria and other cellular organelles is not likely to lead to its revival. However, a number of phenomena have been discovered in recent years that indicate that our concept of an organism as a bag full of genes is an oversimplification. One of these phenomena is the remarkable phenotypic uniformity of most species over vast distances, a uniformity difficult to explain as the result of gene flow. I postulated in my 1963 book that such populations are held together by sharing in a single system of epistatic interactions or, as Waddington would call it, a single system of canalizations, but evidence for the existence of such a system is indirect and entirely based on inference. The study of the distribution of enzyme systems by Hubby, Lewontin, and others is now beginning to open the door to an entirely new realm of research. It seems that the same enzyme loci are variable in many populations of *Drosophila pseudoobscura* and often even have similar allele frequencies. The only exception was a peripherally isolated population. If these findings are confirmed for other species, it would bring us back to the idea that indeed a species may have a species-wide epistatic genic system on which geographic variation and other types of polymorphism are superimposed. It further suggests that this basic epistatic system undergoes a genetic revolution in connection with speciation. It is, of course, far too early to base sweeping conclusions on preliminary results, and the only reason I am mentioning them at all is because they fit so extremely well with some previous postulates.

Let me now cite another door that has been opened onto a *terra incognita*. Until quite recently, when one asked a *Drosophila* specialist how many genes *Drosophila* has, he might have said about 10,000 or, if he was in a very generous mood, 50,000; a mouse geneticist would have given similar answers. Yet, if one measures the amount of DNA in a single mammalian cell nucleus, one finds that it contains enough DNA for about 5 million cistrons, that is, for 5 million genes. It is a great puzzle what the other 4,950,000 genes are doing. We still do not know, but recent studies by Britten and his group in the Carnegie Institution, and by Walker (in Edinburgh) and his group show that there is great heterogeneity in the nuclear DNA and, in particular, that certain genomes may contain large quantities of identical DNA sequences. If such special DNA's should be species-specific, as some of the evidence indicates, it would raise an entirely new set of problems. The reason I am referring to this research is to make it clear how little we still understand what I have previously referred to as the *genetics* of *species*, the very particular genetic structure of species. It is quite possible, if not probable, that the acquisition of isolating mechanisms is merely a coincidental by-product of a far more fundamental genetic event, a genetic restructuring of populations. Only the simultaneous study of several loci or several characters will give us the kind of answers we are looking for. Any day may bring further exciting new discoveries in this area.

Let me now go back to some more classical problems.

The Role of Species in Evolution

The biologist, when he contemplates large-scale evolution, speaks of trends, adaptations, specializations, and invasions of new adaptive zones and niches. The explanation of these phenomena has, however, suffered owing to the fact that the most important part of the story, the role of the agents of these evolutionary phenomena, was omitted. Actually, in each case, it is a species or a group of species that is responsible for the evolutionary events. *Species are the real units of evolution,* they are the entities which specialize, which become adapted, or which shift their adaptation. And speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances. The species truly is the keystone of evolution.

The role of species is to some extent comparable to the role of mutations. Most mutations are irrelevant or deleterious, but whenever there *is* any genetic improvement, it is due to the incorporation of a new mutation into an improved genotype. It is the same with species. Recent taxonomic studies have shown how frequent incipient species are. Speciation obviously is a prolific process, but the majority of new species have a short life expectancy—they become extinct sooner or later. But one out of 100, 1000, or 10,000 makes an evolutionary invention and is able to occupy a novel adaptive zone. Birds, bats, vertebrates, insects, they all ultimately go back to one particular, unusually successful species. Every species is a new evolutionary experiment. Most of them are failures, but an occasional one is a spectacular success. Even when we look at a group of closely related species, we find almost invariably one or the other with an unusual specialization or adaptation. In most cases this merely leads into an evolutionary dead-end street, but occasionally it opens the door to an entirely new world. To repeat, the species plays an enormously important role in evolution.

Species and Ecosystems

One of the unsolved problems relating to species is why some of them, in fact the vast majority, are so narrow in their ecological specialization, while a few species seem to have an extraordinary ecological tolerance. For instance, we can say descriptively that a certain plant host-soecific moth is so specialized that its larvae can live, as leaf miners, only in the leaves of one particular species of plants, while another species of moths has such broad tolerance that it can feed on the leaves of all the species in, let us say, 8 or 10 families of plants. Or to give another example, one species of ants always has small colonies, and only a few of these colonies per unit of area, while another species of the same or a related genus may be extremely successful and become a tramp species that is carried all over the world, establishing colonies wherever it goes. Extremely little is known so far about the reasons for such differences among species. Carson has examined this problem for the genus *Drosophila* and he found that the so-called garbage species, those that can live successfully in most countries, in most climates, and on many sources of food, do, indeed, on the average differ in their karyotype from the less successful, less common, more localized species. But this is only a beginning, and the actual truth of the matter is that we have very little understanding so far of the genetic basis for the tremendous differences in ecological tolerance between different species. It is rather obvious that the classical method of trying to describe species differences in terms of gene frequencies and the fitness of individual genes will not get us very far in such an analysis. The genetics of the ecological role of species is still at its very beginning.

Species and Species Diversity

Up to now I have focused attention on a single species at a time, but there is another aspect to species, and that is the total diversity of species in a given region. To be sure, the total diversity of species at a given place at a given time is the product of the characteristics of all the individual species of which the total is composed. Nevertheless, as in the case of many complex systems, the analysis of the system as a whole gives us new insights into the properties of the component parts, just as the study of the water molecule reveals certain properties of the elements hydrogen and oxygen that the study of these elements in their pure state would not or not easily reveal.

The study of species diversity is one of the most active frontiers of ecology, and the number of unanswered questions is legion. For instance, what is the ecological interaction of species? I think here, in particular, not of such rather simple-minded matters as food chains, but of the far more complex problems indicated by such words as *niche, competition,* and *exclusion.* The niche concept is an old one and even Darwin referred to the "place an animal or a plant occupies in nature" and used other similar expressions. Originally, niche was quite rightly defined as the requirements of a species. In other words, it was designed from the animal or plant outward, as something that the species requires in order to survive and prosper. Unfortunately, there has been an increasing tendency to look at nature as a huge old-fashioned roll-topped desk with an enormous number of pigeonholes, each one the niche of a species. This interpretation leads to many difficulties. There is a far better way of looking at niches, namely, by defining them in terms of the genetic potential of a species to utilize certain components of the environment. The niche, then, is no longer a static property of the environment, but a reflection of the contained species. As soon as we do this, we can understand how the niche utilization can be broadened when a species invades a new area, or in another case how it can be narrowed when the area is invaded by a new species that is more efficient in utilizing certain resources of the environment. There is nothing new in this way of looking at the niche problem, but a great deal of rather sterile controversy could have been avoided by regarding niches as the outward projections of the genetic potential of species. This also helps us understand differences in species diversity between different latitudes. Where violent seasonal fluctuations make high demands on the genetic potential, comparatively few species can cope with the situation, and this is one of the reasons why there are so many fewer species in the temperate zone than in the tropics.

It has always been stated, and qutie rightly so, that successful speciation depends not only on the acquisition of isolating mechanisms, but also on an ability to utilize certain resources of the environment more successfully than any competitor. The species thus is one of the important units of ecology, this importance being due to the fact that any given gene pool has only a limited ecological competence.

CONCLUSION

I am afraid this has been a rather rapid survey of an immensely wide field. The naturalist, the student of local faunas and floras, has understood the importance of the species as a biological unit for hundreds of years. However, the ill-conceived essentialistic and nominalistic philosophies and their translation into arbitrarily defined morphological species taxa has long prevented the full appreciation of the great biological importance of species. This lack of appreciation, I feel, is now a matter of the past. Students of animal behavior and particularly students of species-specific isolating mechanisms have helped in demonstrating the nonarbitrariness of species. More recently, this is being further supported by the kind of genetic studies I mentioned earlier and also by the studies of biochemists and immunologists. I think there can be little doubt that the species represents a level of integration—in the hierarchy of levels from the subcellular to the community—that is of the utmost importance in all branches of biology, particularly in physiology, behavior, ecology, and evolution. It is fully as legitimate to study species as it is to study molecules; indeed, for the healthy integration of all knowledge in biology, it is vitally important that this particular level of biological integration not be neglected. For it is the study of species, more than anything else, that provides a joint interest for some otherwise very different branches of biology, and thus contributes to the unity of biology as a whole.

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