Biological Systematics

BIOLOGY
COLLOQUIUM
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Biological Systematics
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FOREWORD

The Biology Colloquium is conducted in a spirit of informal discussion and provides opportunity for participation from the floor. The colloquium is sponsored by the Oregon State Chapter of Phi Kappa Phi with the collaboration of Sigma Xi, Phi Sigma, and Omicron Nu. Sigma Xi assumes special responsibility for the colloquium luncheon. Phi Sigma and Omicron Nu provide afternoon tea. The College Library arranges special displays of the writings of colloquium leaders and notable works on the colloquium theme.

Grateful acknowledgment is made of the cooperation and interest of the several faculties of Oregon State College that are concerned with biology, of those biologists contributing to the program, of Chancellor Charles D. Byrne, President A. L. Strand, and other executives of Oregon State College.

The first Biology Colloquium was held March 4, 1939, with Dr. Charles Atwood Kofoid of the University of California as leader, on the theme “Recent Advances in Biological Science.” Leaders and themes of succeeding colloquia have been: 1940, Dr. Homer LeRoy Shantz, Chief of the Division of Wildlife Management of the United States Forest Service, theme “Ecology”; 1941, Dr. Cornelis Bernardus van Niel, Professor of Microbiology, Hopkins Marine Station, Stanford University, in collaboration with Dr. Henrik Dam, Biochemical Institute, University of Copenhagen, theme “Growth and Metabolism”; 1942, Dr. William Brodebeck Hermes, Professor of Parasitology and Head of the Division of Entomology and Parasitology, University of California, theme “The Biologist in a World at War”; 1943, Dr. August Leroy Strand, Biologist and President of Oregon State College, theme “Contributions of Biological Sciences to Victory”; 1944, Dr. George Wells Beadle, Geneticist and Professor of Biology, Stanford University, theme “Genetics and the Integration of Biological Sciences”; 1945, Colloquium omitted because of wartime travel restrictions; 1946, Dr. Robert C. Miller, Director of the California Academy of Sciences, theme “Aquatic Biology”; 1947, Dr. Ernst Antevs, Research Associate, Carnegie Institution of Washington, theme “Biogeography”; 1948, Dr. Robert R. Williams, Williams-Waterman Foundation, theme “Nutrition”; 1949, Dr. Eugene M. K. Geiling, Head of the Department of Pharmacology, University of Chicago, theme “Radioisotopes in Biology”; 1950, Dr. Wendell M. Stanley, in charge of Virus Laboratory, University of California, theme “Viruses”; 1951, Dr. Curt Stern, University of California, “Effects of Atomic Radiations”; 1952, Dr. Stanley A. Cain, University of Michigan, “Conservation”; 1953, Dr. Wayne W. Umbreit, Merck Institute for Therapeutic Research, “Antibiotics”; 1954, Dr. Daniel Mazia, University of California, “Cellular Biology.”

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Leader of Sixteenth Annual
Biology Colloquium
Sixteenth Annual Biology Colloquium

Theme: BIOLOGICAL SYSTEMATICS

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R. A. Stirton, Ph.D., Department of Paleontology, University of California

Opening of the Colloquium

Dr. Stephen:

On behalf of the committee and the sponsoring organizations of this Colloquium, I bid you welcome.

This, the sixteenth annual Biology Colloquium, continues the purpose of preceding Colloquia in bringing together outstanding research workers in diversified fields of the biological sciences for the discussion of timely topics. The topic for this year’s Colloquium, “Biological Systematics,” is one of considerable breadth, a topic which would require the better part of several meetings for minimum coverage. Thus, we have had to select that phase of the topic which in our opinion is of greatest significance and upon which marked difference of opinion exists. Our efforts have been directed toward a consideration of the basic elements in our varying systems of classification, the species, and toward the variability expressed by individuals within the species range, the infraspecific categories.

Since the 18th century, we have seen a series of changes, or more precisely, an evolution in concept, on the natural limitations of such units and their modes of origin. The reality of the species and the necessity of the infraspecific categories have been subjected to much criticism in recent years; many of these criticisms are without foundation but a few certainly deserve consideration.

A casual observer, examining systematic catalogs representing the kingdoms, would immediately assume that the concepts in the development of classification systems are essentially similar. A review of the analytical problems faced by the systematists in these fields, however, reveals that such things as ploidy and introgression in plants, asexual reproduction in microorganisms, and the analysis of gross anatomical structures of body fragments in paleontology, make this assumption untenable.

Why then are the mechanics of classification so similar? Is the species an objective or a subjective unit? Should our concepts be directed toward convenience or objectivity? What infraspecific categories are practical in the biological sciences, and do these have an objective reality or are they subjectively practical? Can we hope to devise an all-encompassing species concept for all organisms?

These are but a few of the questions upon which there is little unanimity of opinion. The discussion of concepts by systematic specialists in zoology, botany, microbiology, and paleontology will certainly raise others, but may at least partly resolve some. It is toward such a goal that this Colloquium is directed.

At this time I would like to introduce Dr. A. L. Strand, President of Oregon State College,
whose cooperation and assistance have made this Colloquium possible.

PRESIDENT STRAND:

Dr. Stephen, Ladies and Gentlemen, our Distinguished Visitors from other campuses: The chairman is optimistic if he thinks the college president is going to cut down on his remarks in order to get us back on the timing schedule for his program. But I will try at any rate. In behalf of the College, I am very happy to welcome all of you to this sixteenth Biology Colloquium. Being a sort of a degenerated biologist myself, I am always interested in this affair on campus and at various times have had some comment on the topic. The subject today stops me. I will say, however, that the Colloquium certainly fulfills an important phase in all of the biological sciences. The story of change in man's knowledge, an opinion in reference to living organisms, including himself, composes a very important statement of the story of civilization. The discoveries and conquests in biology have brought about such a revolution in thought that they should be known to all people who aspire to reach some liberal learning. Furthermore, it has been research in the various fields of biology that has changed the life of civilized man to an even greater extent than the common inventions to which we ordinarily attribute the great changes. I think this idea can be defended, for many of us would not be here to enjoy those inventions if it had not been for the discoveries in biology. Thus, the rise of biology through the centuries, especially in the 19th century, which has altered the life of mankind, is an appropriate central subject for examination on any campus.

No doubt the first advances in biology came with the attempts to classify plants and animals. I know that the attempts have been going on ever since. It began with Aristotle, and through the centuries various improvements have been made. In biology, we have gone through the usual cycle of any science, from observation to analysis, and from the experimental method to prediction. In biology, this cycle has taken over 2,000 years. At first, when biologists were largely concerned with just observation and putting things together, they were much more certain than they are today. But the broadening of the field of biology has given rise to hesitation and discussion. The classification of animals and plants has been absorbing to a great many people; it is indeed a very absorbing subject.

All of you have known botanists and zoologists who were so absorbed in their work that they became just a little queer; sometimes hard to get along with. One of the most interesting stories to me of how absorbing the collection of plants can be, was brought back to the campus after the war by one of our men who served in Red Cross work in the Aleutians. I suppose there is no place in the world where living conditions or weather conditions are worse than in the Aleutian Islands. We had many soldiers up there living in quonset huts, about 20' or 24' to the hut, and they didn't have much to do. They read the comics until they got fed up on them, and then they began to read better things. Among them was one man who had studied a little botany, and he asked us for a low powered microscope, some dissecting needles, some collecting flotters, and two or three books that he happened to know about dealing with subarctic flora. Without saying anything to his associates, he began to collect plants on the island where his group happened to be stationed. Of course the other men in his hut thought he was just plain nuts, going around in the spring collecting those little low-growing plants. What sense did that make? But believe it or not, before many weeks had gone by, he began to get some help from the other men in his group, and they became interested in collecting plants. It even developed to a point where they almost forgot the weather. Of course, the officers noted the better morale in that group and encouraged the study of botany as much as they could. Some expeditions were even organized to some of the other islands. Well, the upshot of it was that they did get some new species that had not been collected before, and it made life tolerable to some men who never knew that plants have Latin names or had any names at all, or that anybody was ever interested in naming plants.

Systematics can be an absorbing subject, and it can be a touchy subject too.

Perhaps I had better stop, because if I go on much further, I am apt to attempt a definition of a species myself, and I am sure that would be a major mistake. What little wisdom some of us have is demonstrated by stopping at the right time. We can learn from a lesson from Linnaeus who was the great taxonomist of the 18th century. He originated the binomial system of nomenclature, as all of you know, and it was a great thing for bringing order out of chaos in the classification of plants. Then he went to animals, and it worked equally well there. That is where he should have stopped, but rather he carried it even to the classification of minerals. Of course, he believed
completely in special creation, that in the beginning each individual species of plant and animal and mineral had been created, and nothing had changed since. One old professor of mine tried to make us believe that Linnaeus was an evolutionist, but was too smart to reveal what his thoughts really were. At any rate, he did not stop at the right time, and his attempts to apply his binomial system to minerals was a major error. If I proceed much further I will get into the same situation, so I will merely say that we are very happy to welcome all of you to the 16th Biology Colloquium, and since I won't have another chance, I want to thank the scientists who have come to us from other institutions.

I think that we have had the most distinguished group of scientists on the campus this week since my arrival at Oregon State. In addition to Dr. Oppenheimer, who was here earlier in the week, I want to express my thanks to the men who are here for the Biology Colloquium: Dr. Dobzhansky, zoologist of Columbia; Dr. Lewis, botanist of UCLA; Dr. Stanier of the Department of Bacteriology, University of California; and Dr. Stirton, paleontologist, also of California. As you will notice in the programs, we have been quite dependent upon our sister institutions down the Coast for a good part of the programs of the past Biology Colloquiums. We are grateful also to have such a leader as Dr. Mayr for this Colloquium.

Dr. Mayr was born in Germany. What interested me was he received his Ph.D. from the University of Berlin at the age of 21. His first position was as assistant curator at the Zoological Museum in Berlin, where he remained from 1926 to 1932. Then he became an associate curator of the Whitney Rothschild Collection at the American Museum of Natural History, and remained with that organization for 23 years. Recently he went to the Museum of Comparative Zoology at Harvard, where he is located at the present time. He has always been associated with organizations that have money to organize expeditions, and it has been such expeditions that have added to and stimulated knowledge in biology. Dr. Mayr has spent considerable time in southeast Asia on expeditions to Dutch New Guinea, to the mandated territories in New Guinea, to the Solomon Islands, and I don't know how many other places. He belongs to many important biological organizations, mostly ornithological, in America and abroad. He has published much on taxonomy and the zoogeography of birds. I take great pleasure in presenting the leader of the 16th Biology Colloquium, Dr. Ernst Mayr, who will speak on the subject "The Species as a Systematic and as a Biological Problem."

The Species as a Systematic and as a Biological Problem

**Ernst Mayr**

The title of this Colloquium is "Biological Systematics," and I am sure that there are a few people in the audience who wonder, "Just what is biological systematics?" I am purposely postponing an answer to that question until this evening at which time it will be discussed in detail. By then we shall have gone through the major part of our discussion, and I think an explanation will be much easier. For the present, let me say just a few words on the subject.

Systematics is a science which is the inevitable consequence of the tremendous diversity of nature. Just how great that diversity is, very few people realize. Not only are there thousands and probably even millions of strains of microorganisms, there are approximately a quarter million species of higher plants already described, not counting the cryptogams, and there are nearly a million species of animals known. But even within each one of these species there again is great diversity. There are differences between the males and the females, between various adult and larval stages, between seasonal forms, and between different individual variants that are found in so many species. It is not a rare thing to have as many as a dozen or a score of distinct phenotypes within one species. As a result, there is a staggering diversity of organisms in nature, and this is a challenge to the human mind. A man would like to put some order into this tremendous heap of diverse things, and this is what started classification. The early attempts at classification were somewhat formalistic, merely trying to put similar things together in very much the way, let us say, one puts a stamp collection in order, or might classify the colored pebbles at the beach. But eventually it was realized more and more that dealing with organisms is not the same as dealing with in-
animate objects, and that new methods, new principles, and new concepts are necessary. The classification of organisms, based on the knowledge of their special characteristics, is biological systematics.

Without any further introduction, let me come right to the central theme of this conference, which will be mentioned again and again in the course of our proceedings, the concept of the species. What is a species? If I could define that satisfactorily we could stop right here, adjourn the meetings, and go fishing. However, I'm not going to define it, because I cannot define it in such a way as to satisfy everyone. Whenever I think of the species problem, I am reminded how much difference of opinion there has been and still is.

Hardly a year goes by without the publication of at least one paper and usually two or three on the question, "What is a species?" I recently read a symposium that was published in 1908 in the American Naturalist with a great many speakers participating, all being outstanding biologists of their time. They all had very firm opinions on the subject, disagreeing on nearly every aspect of the problem. But curiously they agreed on one point, and that was that actually species did not exist at all, rather they were something very subjective and purely imaginary; as one of them said, "a figment of the human imagination." The reaction was that in the following period people went to the other extreme, insisting almost like Linnaeus on the fixity, constancy, and objectivity of species.

I have been working with species for something like thirty years, and like all other people who deal with species, I have been thinking about the species problem, worrying about it, and trying to do something about it. And I've sinned like all others and have proposed species definitions; and have then gone on and wondered whether they were right. It is only within the past two or three years that I have discovered one of the main reasons for such diversity of opinion: we have not just one species concept, but three. This may be an unorthodox and somewhat startling conclusion, and I now feel obliged to give you my evidence. Before I do that, however, let me say one word on the matter of method. We must make a clear distinction between concepts and the applications of these concepts. We can have a concept "stream," for instance, but there will be some argument whether the little brook which runs through your back yard is a stream or not, or whether an ocean current like the gulf stream should be called a stream. Or let's take another case—the concept, "tree." Nobody will deny that the concept, tree, exists. But then you take a creeping juniper or you take the famous tropical plant, the strangling fig, and you begin to wonder whether you are justified in applying the concept, tree, to these phenomena.

It is the same with species. We can, I believe, develop precise and specific concepts of the species, but we may have a great deal of difficulty in applying these concepts to concrete situations.

What are the three concepts of the species that I have the temerity to claim exist? The first one goes back to Plato and probably farther than that; it is nowadays referred to as the typological concept. Those of you who have studied Plato remember the "eidos" he talks about, as being some definite type of thing. The word "eidos" has been translated in Latin into the word "species." It is a concept that is still widely in use in the fields where one deals with the classification of animate objects; the mineralogist speaks of "species" of minerals; the physicist speaks of "nuclear species." Now all of these usages have common ground in that they define species as "something different," "a different thing." The emphasis throughout is on the difference, and Plato in a way denied variability when he insisted that the "eidos" was the real thing and all the observed variations were, to use his simile, "shadows on a cave wall" cast by the object itself. In biology, the typological species concept is usually referred to as the morphological species concept. A species is something that is morphologically different, and in early taxonomy this was the species concept. Even today, it is an important concept, and in many situations where no other species concept can be applied, we still have to depend on this morphological species concept. However, this concept has a great many difficulties, two of which I shall mention in particular. One is that very often it does not work too well. For example, let us take a caterpillar and a butterfly. No one will question that these are two different things, two very different things. If you were to apply the morphological species concept consistently you would have to classify the caterpillar and the butterfly as two different species, which of course, is biological nonsense even though it has been done. Linnaeus himself was often fooled in such cases of morphological difference of different forms of a species. He classified the male and female Mallard (Anas platyrhyncha) as two separate species. Likewise, he classified the immature and adult goshawk as two species, because they were different. But as soon as these relationships were established, Lin-
naeus himself abandoned the purely morphological species concept. We also have the opposite objection to the morphological species concept, namely that two forms which morphologically are virtually identical can be shown by other criteria to be different species. Professor Dobzhansky will tell us about such a case in his discussion of the genetic aspects of the species. Here again the morphological species concept breaks down. However, not only are there practical difficulties to this morphological, typological species concept, but what is more important is that this concept ignores the fact that organisms consist of populations, with their interbreeding, with their genetic variability, with their evolution, and with all the other features that characterize organisms. It is absurd to apply to them the same concept as we apply to invariable objects of inorganic nature.

The arbitrariness and the subjectivity of the morphological concept were subjected to such criticism that we realized something was wrong. Whenever people say species are something purely imaginary, something purely subjective, very often what they have in mind is this morphological, typological species concept. When I read papers ridiculing the existence of species, I always remember an experience that I had during my collecting days in New Guinea. I apologize to those of the audience who have heard this before. Some 25 years ago, when I was in the mountains of New Guinea I was all alone with a tribe of very primitive mountain Papuans, who were excellent hunters. I sent them out every morning with their guns, and for every specimen that they brought back I asked, “What do you call this one?” I recorded the scientific name in one column and the native name in another. Finally, when I had everything in the area, and when I compared the list of scientific names and the list of native names, there were 137 native names for 138 species. There were just two little greenish bush warblers for which they had only a single name. At the time, I took this for granted because as a naturalist I always believed in species, but whenever I read statements by armchair biologists who deny the existence of species, I always marvel at the remarkable coincidence that the scientist and the native in New Guinea should by pure accident have an imagination that is so closely similar that they assign the mountain birds of New Guinea to the same number of species. Of course, in our local fauna here, we have the same phenomenon. If we go out and study birds in the woods around Corvallis, or mammals, or beetles, or plants, we find that normally we can classify them without any difficulty into well-defined species. As an example, I’m showing you a slide from Peterson’s Field Guide of Birds, depicting the five species of thrushes of the genus Hylocichla. There are the wood thrush, the hermit thrush, the veery, the gray-cheeked, and the olive-backed thrush. A glance at the slide will convince you that on the whole they are very similar. They usually have a spotted breast, the upper parts are a sort of grayish-brown or rufous, and some of the species, particularly the gray-cheek and the olive-back, are exceedingly difficult to tell apart unless you are expert. Now, what about the distinctness of these five species? If you go out in the woods and study them, you find that they differ in their song, in their nests and eggs, in their migration, and, to some extent, in their food. In summary, if you study their biology and ecology carefully, you find that in every single respect these five species are different. Even though as many as three of these species may be found in the same area, nobody has up to now found a single intermediate or hybrid. They are well-defined, they are separated by clear-cut gaps, called by Goldschmidt “bridgeless gaps.” They are What we call “reproductively isolated” (Figure 1).

What is the particular lesson we can draw from this? It is that if we are at a given locality without the time dimension, without the dimensions of longitude and latitude, at such a spot species are clearly defined. In such a nondimensional situation, species are characterized by a reproductive gap, and they are characterized by a particular relationship to each other, namely, that of noninterbreeding. This is a completely objective criterion which applies to species at a single locality, namely that they have a definite relationship to each other—that of not interbreeding. It can be just as objectively defined as the relationship “brother.” If I look at any male member of the audience, I would not know whether he is a brother because it is not one of his obvious external characteristics; it is something that has a meaning only in relation to some other sib of his. Likewise, the real meaning of the species of a single locality is in the property it holds in relation to some other species. As valuable and as objective as this species criterion is, it faces a number of difficulties, particularly in its applications. The first one arises from the very factor which makes species distinct at a locality and which gives them an internal cohesion. It is the fact that they are formed by populations of interbreeding individuals. It is this interbreeding, which gives the
Figure 1

The five species of thrushes of the genus *Hylocichla*

species its cohesion, and the noninterbreeding which sets it apart from the other sympatric species. At once it becomes obvious that we lose our most important criterion of the species in cases where there is no sexuality. It becomes very questionable, in fact it becomes quite impossible, to apply this second species concept, this nondimensional or, as it is sometimes called, biological species concept, in any case where sexuality is definitely absent.

A second and more frequent difficulty is that in the practical work of taxonomy we rarely deal with species that have no dimensions of time and space. Rather, we attempt to classify populations collected at many different localities. What shall one do with a series of contiguous populations where each population is interbreeding with its neighboring populations, but which have become more and more different until the terminal populations look like different species? The addition of the dimensions of longitude, latitude, and time often creates formidable difficulties. For example, the common song sparrow, *Melospiza melodia*, is not restricted merely to the locality where it was first described in the Eastern United States but extends all the way from the Atlantic to the Pacific and from Alaska and the Aleutian Islands down to Mexico. An extensive distribution is true for the majority of species, and it leads to a third species concept, namely that of the multidimensional species or polytypic species. This species is defined as an assemblage of interbreeding populations in which there is an active gene exchange.

Here we have a third concept of the species, which is a *group concept*, not like the second concept, one of relationship. It is a collective concept, described by the gene flow that goes through this system. This third concept likewise has its practical limitations. It works well as long as there is complete continuity of populations and the difference between them is not too great. But as soon as we have to decide whether or not certain more or less isolated populations belong to this system, we lose the objectivity because we have to make judgments and can no longer apply the objective yardstick of interbreeding or noninterbreeding. This third concept is very distinct. In a few minutes we shall see how all of these concepts are connected with each other and to what extent they reinforce or contradict each other.

But first let us ask whether there are any more species concepts? It would be surprising if there were not, but frankly speaking I cannot think of any additional ones. Several others are mentioned in the literature, but they are not truly different. Some authors have referred to the "genetic species concept," but geneticists have applied genetic criteria to every one of the three concepts I have mentioned. The early Mendelians thought of the new species in a typological way. Some, like De Vries, thought that a single mutation could create a new species. Other geneticists quite rightly have emphasized the isolating mechanisms between species, particularly genetic sterility barriers, and have proposed genetic species definitions which coincide with the second, the nondimensional species concept I mentioned. Again, geneticists have emphasized the gene flow through the collective, the polytypic species, leading to a genetic criterion of the possibility of gene interchange of the populations belonging to a species. Again, this is not a separate genetic species concept.

Thus, we have three concepts, seemingly in conflict with each other. How can we reconcile them in the practical work of the taxonomist?

The morphological concept, as I stated once before, has always played second fiddle because even Linnaeus, whenever he found a conflict between the morphological concept and the biological facts, invariably abandoned his morphological concept. Why then don't we discard it? The reason is that there are many situations where we lack the information to apply the biological species concept. In asexually reproducing organisms, for instance, one is generally forced to apply morphological criteria and apply a morphological concept. In the case of geographically isolated populations we are likewise forced to apply morphological criteria. For example, the song sparrow, that I mentioned earlier, occurs in one population on the Aleutian Islands, where it is isolated from the mainland population. In order to decide whether this Aleutian sparrow is a song sparrow or not, we have to rely to a considerable extent on the amount of difference it shows as compared to the mainland population, and the amount of difference among different populations within the mainland species. The paleontologist, as we shall probably hear this afternoon, also has to rely extensively on morphological criteria. This is not at all to be deplored, because after all the morphological differences between species as well as the morphological similarities of populations within species are caused by genetic factors and are thus an indication of the amount of genetic difference. Furthermore, we have come to believe that within a group of related forms there is a considerable amount of correlation between the degree of difference in
genes that causes morphological differences and such genes that control reproductive isolation between species. Thus, we now assume, if we know the particular group well, that a certain amount of morphological difference very often is indicative of reproductive isolation in cases where we cannot test it otherwise.

What about the relation of the nondimensional and the collective species? We find that we need both of these concepts to define species and the more widely accepted modern species definitions invariably incorporate both of these concepts. The species is usually defined in some such terms as: "species are groups of actually or potentially interbreeding populations" (this would be the collective species concept) "which are reproductively isolated from other such groups" (that would be the nondimensional biological species concept). Thus, in actual practice we combine these two concepts, yet we must realize that in many ways the two concepts are different. Many of the arguments in the literature on the species problem are due to the fact that one author is talking of one concept and the other author either about the other one or a combination of the two. In practice, we very often get into considerable difficulty because of a conflict between these two concepts. The best-known case for this is the situation often described as "circular overlap" which I will presently illustrate with two slides (Figure 2).

Suppose we have a population of a species and it spreads around in a circle until it returns to the area from which it started so that we now have an area with an overlap of the final links in a long chain of populations. If, in the course of this expansion, the gene content of these populations has continuously changed to such an extent that isolating mechanisms have developed we have in the area of overlap two reproductively isolated populations. Examined from the point of view of the nondimensional species concept, we have obviously two different species because they are reproductively isolated from each other. On the other hand, if we take the collective species concept—i.e., gene flow between interbreeding populations—as the species criterion, all the populations on the overlapping circle belong, of course, to one single species. Don't ask me to solve this conflict for you, because actually there is no solution for it. This is a trick that evolution has played on us, a trick for which there is no solution.

Here then is one of the conflicts between the nondimensional and the polytypic species concept. I do not want to say any more about the application of the species concept in paleontology, microbiology, or botany, because we will hear about this in other contributions, but let me say just a few words about the subdivisions of the species. Here again a great deal of controversy occurs in the literature, and we can not hope for agreement unless we first clearly establish a few principles.

The first one is that there is a tremendous difference between sexually and asexually reproducing organisms. The population is the central theme of variation within the sexual species and cohesion within the population is the result of sexual reproduction. Lack of sexual reproduction prevents the occurrence in asexually reproducing organisms of something that would correspond to a population. There are only strains or lines or clones. The second point is that two kinds of variation within the species must be distinguished, individual variation and group variation. As a consequence, we recognize categories that are set up for individuals like albino, or blue-eyed people, in the human species, and categories that are based on true populations, like races, and this is reflected in the currently accepted terminology. The original infraspecific terminology of the early taxonomists was affected by their typological species concept. Every individual within a species that did not conform to the type was called a "variety." At the present time, there is a strong trend to abandon the term variety altogether because it was indiscriminately applied both to populations which, if they are different enough, are now called subspecies, and to individual variants.

The most commonly used infraspecific category in modern taxonomy is the subspecies. This term has recently been the target of a good deal of criticism and there are a few younger people who would like to throw it out altogether. A figure of the distribution of the golden whistler in the Solomon Islands may serve to indicate what difficulties it would lead to if we would try to describe variation in species without utilizing the concept of subspecies. Some, for example, might suggest simply to refer to the various forms by the name of the island on which they occur. This is hardly workable for in some cases the same form occurs on two or three different islands, like P. p. orioloides on Choiseul and Ysabel. Such a designation by locality is certainly not very revealing and not very useful. The other suggestion that was made was to ignore the taxonomic subdivisions of the species altogether. In so doing, we would certainly lose a great deal of information. This is demonstrated in the case of the pied wag-
Figure 2

Map showing distribution and circular overlap of *Hoplitis producta*. The zone of intergradation between *producta* and *interior* is shown by overlapping types of shading. Intergradation between other subspecies is either little known or so gradual and occurring over so broad a zone it cannot be shown well on a map such as this. (Modified from Michener, 1947, "A Revision of the American Species of Hoplitis (Hymenoptera, Megachilidae)." *Bull. Amer. Mus. Nat. Hist.* 89 (4).)
tail Motacilla alba, of the Old World, a species extending from the British Islands through Europe, Persia, Tibet, Siberia, Northwest China, Kamchatka, to Japan. All these forms are markedly different, some having very extensive ranges, others having rather narrow ranges. The area of intergradation between a few is very narrow, but in other cases it is very extensive. All I can say is that if we were either to ignore geographic variation or try to indicate it merely by geographical designation, we would lose a great deal more than we would gain. The subspecies is not an ideal category, but in many cases we can not do without it. On that basis, we can define subspecies, perhaps, as geographically delimited aggregates of local populations which differ taxonomically from other such subdivisions of species.

In addition to the subspecies there are two or three other infraspecific terms in use. Most widely cited is the term ecotype, which is used extensively in botany. The ecotype is usually defined as a local population or race, which owes its phenotypic characteristics to the specific climatic or edaphic factors of the environment. Actually, there is no basic, no conceptual difference between the geographic race and the ecotype. In both cases we are dealing with populations that have a spatially defined area of distribution, only in the case of the ecotype the correlation between the environment where this population occurs and the phenotypic characters is more obvious than usually in the case of subspecies (Figure 3).

We are now ready to summarize two or three of the more important points that we have tried to establish up to now.

The first one is that taxonomy within recent decades has moved progressively away from a purely formalistic treatment of the diversity of nature and has tried to determine the biological significance for the various subdivisions above, at, and below the species level.

The second one is that we actually deal with three somewhat independent concepts when we speak of species, and many of our difficulties are due to a conflict between these three concepts.

Among the infraspecific categories the only one with biological reality is the population. Every local population of a sexually reproducing species is somewhat different from every other one, genetically as well as in other characteristics. It is adapted for the particular local environment, and if a morphological analysis is carried far enough biometric differences in morphological characters will be found. As soon as we group together such populations into units which we call subspecies or ecotypes, we add a subjective element and lose the objective reality that we have in the case of the biological species which is objectively defined by the phenomenon of noninterbreeding with other sympatric populations.

The task of the other speakers of this symposium will be to see whether the material on which they are working yields similar conclusions or, what would be more interesting, whether the diversity of nature would lead them to conclusions which contradict mine.

DR. STEPHEN:

Thank you, Dr. Mayr. We anticipated a slight delay in the submission of written questions. The apparent lack of questions attests to your excellent presentation. Ecotypes themselves seem to be one of the most critical nomenclatorial problems that we face. Some of the criticisms that have been presented against the subspecies are directed at the ecotype. Do you consider ecotypes, which are phenotypically similar, yet have distinct distribution patterns, as the same subspecies?

DR. MAYR:

The subspecies, I believe, is merely a practical means of the taxonomist to classify populations in a convenient way. Every subspecies is a collective
unit even where the ranges of these populations are continuous and contiguous. To give different names to indistinguishable populations because they do not have continuous ranges may seem like a more honest solution than to lump them under the same name, but such a procedure would imply that the subspecies is a biological unit, which I believe it is not. The main object of the subspecies is to permit the taxonomist to put in order phenotypically different populations within the species. In plant taxonomy, likewise, it has been customary to combine similar looking ecotypes under one name even when they did not have continuous ranges. This would seem a logical procedure. As the subspecies is an aggregate of taxonomically similar populations, it would seem best to adopt an equivalent solution for ecotypes. Similar appearing ecotypes should be combined under the same name even where their ranges are discontinuous.

**Dr. Stephen:**

In my opinion, that leads to an inherent difficulty. For example, we have disjunct, phenotypically identical, mountain top ecotypes of a species of continuous range. Or, we have subspecies designated which are nearly identical phenotypically, yet are at opposite ends of the range in a species cline. Do we still apply the same subspecies name to these two ends where this occurs? Can we be purely subjective, or should some degree of objectivity come into consideration?

**Dr. Mayr:**

No general overall answer can be given to all these questions. One has to decide these matters from case to case. If you have a continuous range and you give the terminal populations different subspecies names, even though they are indistinguishable, then you will arouse the justified ire of those who do not believe in subspecies. They will say, this man is so anxious to name things that he even names populations that he himself says he cannot tell apart. You will have to decide in such a case where do you gain more, by not naming or by naming them? You know that these populations are different genetically, but you also know that they are not different morphologically. You likewise know that populations within continuous ranges of subspecies are also different genetically. The only difference between the two situations is that in one case the ranges are continuous and in the other, discontinuous. I am personally inclined not to give different subspecies names to populations that cannot be told apart.

**Dr. Stephen:**

Yet, we have species which are morphologically identical, but from their habits we realize that they are specifically distinct. Shouldn’t some of the objective analyses of subspecific groups be undertaken?

**Dr. Mayr:**

At the species level, owing to species concept number two, we have an objective criterion. Two sympatric natural populations are different species by definition because they are noninterbreeding entities. When we have that fact established we do not need additional morphological criteria. But on the infraspecific level, when you are dealing with aggregates of populations, you have only one criterion, that of morphological difference, and if that is absent, then you have nothing left for nomenclatorial distinction, even where you are convinced that there are genetic differences. I don’t think there is any ideal solution. It is a thing that everybody will have to decide on the basis of what his conscience tells him to do.

**Question:**

Would closely related species, such as the five thrushes shown on the slide, which maintain perfect separation in nature interbreed in captivity? If so, would one obtain sterile progeny as in the mule? If they do produce fertile progeny, could not these lead to the formulation of subspecies?

**Dr. Mayr:**

Fortunately, this is an easy one to answer, because we have many cases where perfectly good species in nature are completely fertile with each other in captivity. Many members of the audience will know the two very common ducks, the Mallard and the Pintail. They are perhaps the two most common fresh water ducks in the entire world; they coexist over the entire northern hemisphere, both in the new world and the old world, breeding in the same marshes, ponds, and creeks, virtually never hybridizing. However, breeding experiments have shown that in captivity they will interbreed readily. According to Phillips there is no reduction of fertility at all in the F1 and in the F2 or in the backcross. The same has been found by Carson for a species pair of Drosophila in South America. It is true for many ducks and for quite a few gallinaceous birds, and is probably a widespread phenomenon. This fact seems to account for one of the major differences between plants and animals. While the sterility barrier is perhaps the most important barrier between co-
existing species of plants, in animals the noninterbreeding of sympatric species may be maintained by many devices. These devices have been designated by the general name of isolating mechanisms, a very appropriate term coined by Dobzhansky. Among the isolating mechanisms in higher animals are numerous behavior elements, "psychological factors," as they are sometimes referred to. Thus, the Mallard and the Pintail do not interbreed in nature because, to put it crudely, they don't like each other. If a male Mallard in the field meets a female Pintail, or vice versa, they just don't look at each other. They don't consider each other "conspecific." There are many cases where perfectly good species are separated by adequate isolating mechanisms without sterility. They are adequate because they prevent the occurrence of hybrids under normal conditions. Ask any avid duck hunter who has shot Mallards and Pintails, how many hybrids he has found. Most likely he has never found one, because I think roughly only one hybrid occurs in about a hundred thousand birds shot every year. It is a very small ratio. The few hybrids are apparently sufficiently aberrant, either ecologically or psychologically, so that they do not backbreed with either parental species. So here you have perfectly adequate isolating mechanisms without any known sterility factors.

**Question:**

Could the hybrids be considered incipient subspecies?

**Dr. Mayr:**

They cannot because a subspecies is a geographically defined subdivision of the species. Hybrids, on the other hand, coexist with the parental species, and if not sterile or inviable they will be absorbed in the two parental species. Then we would have what Anderson calls introgression. Introgression apparently occurs fairly frequently in plants, but in the higher animals there are only about one dozen well-established cases known. A breakdown of isolating mechanisms between two good species can not lead to the formation of subspecies. Of course, if two strongly different, geographically representative (allopatric) populations meet in a border zone, they will form an intermediate population which taxonomists have sometimes described as a subspecies.

**Dr. Margach:**

Do species have a more ultimate reality than subspecies? In other words, are species real biological categories while subspecies are only practical categories?

**Dr. Mayr:**

The answer to this question is very definitely yes. There are, of course, some subspecies which have completely definable reality. Perhaps I should not use the term "reality," in view of the objections of some philosophers. But as biologists we know what we are talking about, so I'm going to continue using this somewhat ambiguous word. An individual subspecies may have a well-defined reality, if it is an isolated population, as for instance the song sparrow of the Aleutian Islands. But the subspecies, as a concept, does not have reality because it is a purely subjective matter as to how many populations are placed into one subspecies. The lumper will have a great many different populations within one subspecies and the splitter may separate each of these populations into a different subspecies. There is no objective criterion which would give the subspecies the reality of the species objectively based on the gap of noninterbreeding maintained by the isolating mechanisms, which in turn have a genetic basis. Here is something which can be defined objectively and which the species themselves respect, because otherwise they would grade into each other. At any given locality, every species is well-defined against the others, and this is what a biologist would call a reality.

**Question:**

Do not the categories "subspecies" and "species" intergrade?

**Dr. Mayr:**

We would expect such intergradation to occur if subspecies have the ability to evolve into species. Quite obviously this is correct. As I tried to show, this is precisely where conflict arises between the three species concepts. Every geographically isolated portion of a polytypic species ("geographical isolate") is an incipient species. If such an isolate is phenotypically different from the main body of the species, it is a subspecies which is simultaneously an incipient species. Obviously there is a complete and very gradual intergradation between isolates which have not reached species level.
Specific and Infraspecific Categories in Plants

HARLAN LEWIS

It is indeed a great pleasure for me to have this opportunity to visit this campus and discuss with you a favorite topic of mine. The title is a simple one and suggests that it might be dealt with adequately by defining the categories concerned, making a few generalizations concerning the means of delimiting them, and using a few appropriate examples as illustrations. The topic has many facets, however, and cannot with justification be treated so summarily. I do not propose, therefore, to cover the subject exhaustively this morning. You will not, for example, be provided with a definition of species and subspecies, and, unlike Professor Mayr, I will not take the opportunity to inflict one upon you later in the day. I shall, however, attempt to indicate to you the nature of these categories as they are delimited in actual practice. For this purpose I shall draw heavily, and undoubtedly with prejudice, upon my own experience and intimate acquaintance with a very limited number of species belonging to a few genera. Consequently, I make no pretence of speaking for all plant taxonomists.

Taxonomic categories have two functions in modern biology. One is classification for the purpose of communication. The other is to indicate a certain degree of genetic relationship. Categories are delimited and a classification achieved by phenotypic discontinuities. On the other hand, genetic relationship is inferred from phenotypic similarities, although in certain instances, particularly at the infraspecific level, this relationship may be determined from experiment.

A comparative study of external morphology provides the principal data from which the taxonomist of flowering plants delimits the various taxa. His primary source of material consists of desiccated samples deposited in herbaria. A taxonomy based upon such material has limitations, even from the standpoint of comparative external morphology, because some traits, such as flower color and certain aspects of habit and texture, may be altered or completely destroyed in the process of pressing and drying. But the taxonomist is aware of this limitation and when feasible supplements his study of herbarium material with a careful examination of the morphology of living plants. Since pre-Linnaean times, living specimens in botanical gardens have been an important adjunct of major botanical institutions. It has also been frequently noted that herbarium samples may not be representative, depending upon the vagaries of the various collectors. For example, one is likely to find a disproportionately high percentage of aberrant individuals, a bias toward specimens that fit nicely on a standard herbarium sheet, linear distributions following major highways, and an abundance of specimens from such scenic localities as Yosemite Valley. Despite these limitations, a careful examination of herbarium material is still the way to initiate a taxonomic study. Today, with rapid transportation, particularly by automobile, it is possible for the taxonomist working on groups that grow within a few hundred miles of his base of operation to study large numbers of living plants in their natural habitats and to obtain representative samples for morphological analysis.

The question of classification presents itself even though the plant taxonomist has access to only very limited morphological and geographical data, perhaps from a single specimen. How different must two groups of organisms be before they should be designated as species? My botanical "grandfather," so I have been told, had a simple formula as a solution to this problem, namely, if two taxa differed by one character they were forms; if they differed by two characters they were subspecies, and, if they differed by three characters, they were species. I am obviously a renegade because I was recently author of a species that differs from its nearest relative, after careful statistical scrutiny, by only one character of external morphology (Lewis and Lewis, 1953). The fact still remains, however, that species are separated by clearly evident phenotypic discontinuities. Dobzhansky (1951) has made explicit the basis for the maintenance of the integrity of these discontinuities as a consequence of barriers of various kinds to gene exchange, operating either singly or, more frequently, in combination. The firm establishment of this principle has contributed greatly toward a better taxonomy as a result of the orientation that it has provided for the taxonomist. In fact, the experimental and cytological approaches, which the taxonomist frequently employs today to supplement morphological studies, are designed primarily to demonstrate the presence, or absence, of barriers to gene exchange between phenotypically recognizable.
groups. Consequently, it is not surprising that the more recent techniques have validated, more often than not, the taxonomic conclusions reached earlier by astute taxonomists using only comparative external morphology.

An obvious corollary of the principle that the integrity of a species is maintained by barriers to gene exchange should be emphasized. Namely, sympatric association of phenotypically distinct groups of organisms can be taken as evidence of effective barriers to gene exchange, without experiment, unless, of course, the discontinuity is attributable to simple genetic segregation. Sympatric association in flowering plants means coexistence within the normal effective pollinating range of the species concerned.

Sympatric distributions afford the taxonomist with a very useful tool which in the past he has too often neglected. One frequently finds in taxonomic works, particularly in the floras in current use, reference to infraspecific taxa, usually referred to as varieties, that are said to grow together or "with the species." These are immediately suspect. We have had occasion to look into several of these cases and have found them to be of three sorts. First, the entities differ by simple segregating genetic factors; second, they are comprised of self-pollinating or asexual strains or, third, they are distinct species, which may, however, differ by few or inconspicuous morphological traits.

With these introductory remarks let us now examine several patterns of phenotypic differentiation and consider their taxonomic resolution by way of illustrating the diverse nature of species in different genera of flowering plants. In these examples we shall consider only the diploid, sexually reproducing and normally outcrossing representatives of the groups concerned.

A frequently encountered pattern is one that can be illustrated by the genus *Trichostema* (Lewis, 1945) in the mint family (the common local representative is known as vinegar weed). The diploid taxa in this genus are distinguishable by clear-cut and obvious morphological discontinuities such that all individuals we have encountered can be placed without hesitation into a particular group. The morphological discontinuity between many of these groups is comprised of numerous traits involving nearly every part of the plant. The number and diversity of the morphological differences are such that one has confidence that, by any criterion, each of these groups belongs to a distinct species. But other groups, as for example *Trichostema lanatum* and *T. parishii*, differ from one another by discontinuities in only a few traits. From the standpoint of classification for the purpose of distinguishing between them, it makes no difference whether we call them species, as I have indicated, or whether we call them subspecies. But for the purpose of indicating whether or not the two groups constitute genetically independent systems, the category to which they are assigned has significance. In this particular example, the two taxa replace each other geographically, which suggests that they might represent geographical races of the same species. Their distributions, however, do overlap in one small area. In this area cross pollination is known to occur, but no hybrids have been found. The specific status of these two taxa seems thereby assured. But other equally similar taxa may be allopatric. The fact that they do not grow together is, of course, an effective barrier to gene exchange, but one that may be temporary and not necessarily indicative of genetic divergence, although it may be an important factor in promoting such divergence. Internal barriers to gene exchange can be inferred to exist between some allopatric groups from a study of their karyotypes. Chromosomes, because of their significance in heredity, do not, of course, indicate the absence of such barriers. The presence or absence of internal barriers between allopatric groups can be determined by suitable experiments. But many plants do not lend themselves to experiment and in these instances the problem of allopatric taxa, such as the island distributions just discussed by Professor Mayr, must be resolved on the basis of experience gained from a study of related groups.

The morphological discontinuity between species is not necessarily evident in any one trait, as can be illustrated by two closely related species of *Clarkia, C. unguiculata* and *C. exilis, in the evening primrose family. These two species occur sympatrically and are genetically incompatible. One hybrid, which was highly sterile, has been produced in the garden, but only after many unsuccessful attempts (Lewis and Vasek, 1954; Vasek, 1955). The two species differ in the mean expression of many traits, but the variation is such that the extremes of any one trait overlap. They do not differ by any one, clear-cut, morpho-
Figure 4
Geographic distribution of five closely related taxa of the genus *Clarkia*
logical character. Nevertheless, I recognized Clarkia exilis as a species distinct from C. unguiculata when I first saw it, although at the time I was driving past at 20 miles an hour. I mention this to illustrate that in summation of morphological traits the two species are sufficiently distinct to be readily recognizable. The summation of differences that we recognize immediately upon inspection can be indicated graphically by a simple process of additively combining several easily measurable differences. In the present case, if one combines the five or six traits that show the greatest mean differences and the least overlap, one can show a distinct morphological hiatus between the two species with no intermediates except for the one hybrid so laboriously produced (Vasek, 1955).

In contrast to the well-defined morphological discontinuities exhibited by the examples we have discussed, the pattern of morphological differentiation that Professor Carl Epling and I have studied in a group of Californian delphiniums is very different (Lewis and Epling, 1954; Epling and Lewis, 1952). The morphological extremes differ by numerous conspicuous traits such as stature, branching habit, pubescence, leaf shape, and the size, color, and conformation of the perianth. Any observer would, I believe, certainly recognize populations of these extremes as belonging to distinct species. But in addition, one finds a series of morphological modes in which the traits that characterize the extremes are variously combined. Furthermore, these modes are not sharply differentiated from one another. The reason is not difficult to find, for individuals representative of the various morphological modes are interfertile to a relatively high degree, that is, not only are F₁ hybrids obtained easily but they in turn yield large and vigorous backcross progenies. If these groups of delphiniums replaced one another geographically the pattern would be that of a polytypic species, such as is frequently found among animals. But in these delphiniums each of the morphological modes occurs sympatrically with at least one other. Furthermore, the pollinations that we know will produce fertile hybrids in the garden actually do occur in nature. The principal pollinators are bumble bees, which we have frequently seen visiting morphologically very different delphiniums in succession in the wild and in the garden. Consequently, the avenues for gene exchange are seemingly wide open. Nevertheless, the constellations of characters by which one distinguishes the various modes have maintained their integrity, except for a limited number of intermediate individuals, despite sympatric association for an undeterminable length of time, but assuredly one measured in terms of many generations. The most important factor contributing to restriction of gene exchange between the various modes is ecological. Where two or three of them grow side by side, they show a differential response to particular seasons. The principal morphological modes in Delphinium we call species, even though the genetic and morphological discontinuity between them is not sharply defined. Interfertile sympatric species are not, however, unique to Delphinium but are known in a number of plant genera, for example, Salvia, Penstemon, and Aquilegia, to name but a few.

Some patterns of differentiation can be definitively resolved only with information derived from experiment. A group of closely related taxa in the genus Clarkia will serve to illustrate. These taxa can be referred to as brandegeae, biloba, australis, lingulata, and dudleyana without designation, at present, of taxonomic rank.

Geographically, brandegeae, biloba, and australis replace one another, from north to south respectively, in the Sierra Nevada foothills (Figure 4); lingulata is known only from two colonies adjacent to australis and probably within pollinating range of it; dudleyana grows in mixed colonies with lingulata, australis and biloba, but not with brandegeae from which it is separated by a linear distance of 75 miles.

The more conspicuous morphological differences between these five taxa are summarized in Table 1. From this table it can be seen that brandegeae closely resembles dudleyana; the two are indistinguishable vegetatively and are similar in flower, except for the petals of brandegeae, which are usually shallowly lobed and of uniform color (aside from flecking characteristic of all the taxa). In contrast, the petals of dudleyana are
usually entire and streaked with white. But the petals of *brandegeae* are occasionally entire and those of *dudleyana* are sometimes shallowly lobed and of uniform color. Individuals of each are found that cannot be identified with certainty on the basis of external morphology. The morphological differences between *brandegeae* and *biloba* involve leaf shape, the habit of the inflorescence, and particularly the shape and color of the petals. In their mean expression, they are conspicuously different taxa, but intermediates are found in the area where they come together. *Brandegeae* differs from *australis* and *lingulata* in several traits. *Biloba* is sharply defined by vegetative and floral characters from *lingulata* and *dudleyana*; *biloba* and *australis* differ in the mean expression of several traits but are connected by intermediate populations. *Australis* is sharply defined by many traits from *dudleyana* but differs from *lingulata* in only one discernible trait, namely, the shape of the petals, which are conspicuously lobed in *australis* and entire in *lingulata*. The difference between *lingulata* and *australis* is such that it might be due to a single gene. Aside from this simple but sharp discontinuity in petal shape, one finds a morphological continuum in the sequence *lingulata-australis-biloba-brandegeae-dudleyana*. This sequence also indicates the relative morphological similarities, with *lingulata* and *dudleyana* bearing the least resemblance to one another and with *brandegeae* morphologically more similar to *dudleyana* and *biloba* than to *australis* or *lingulata*.

On the basis of external morphology alone one might consider all of them as components of one polytypic species with *lingulata* as a simple genetic deviant, or form, of *australis* and the remainder morphologically integrating subspecies. But other considerations alter this picture. For example, the sympatric occurrence of *dudleyana* with *lingulata*, *australis*, and *biloba* indicates that two species are involved. The status of *dudleyana* as a distinct species from *australis*, *biloba*, and perhaps *brandegeae* is further indicated by an examination of chromosomes; *dudleyana* has a haploid number of 9 whereas the others each have 8. One also finds that *lingulata* has a haploid number of 9, which further distinguishes it from *australis*.

Information concerning genetic compatibility and relationships, as indicated by hybridization, contributes further to our understanding of these taxa. We have been unable to obtain, after innumerable attempts, a mature hybrid between *dudleyana* and any of the others, thereby substantiating its status as a distinct species, despite the occurrence of individuals that are not clearly distinguishable from *brandegeae* in external morphology. All of the other hybrid combinations are easily obtained in the garden. The hybrids *brandegeae x biloba* and *brandegeae x australis* are 50 per cent fertile; *brandegeae x lingulata* is about 20 per cent fertile (Table 2). *Biloba* and *australis* are completely interfertile, whereas both of these form hybrids with *lingulata* that are about 10 per cent fertile. *Lingulata*, then, not only differs from *australis*, *biloba*, and *brandegeae* in petal shape and chromosome number, but also forms hybrids of low fertility with them. These facts warrant, in our estimation, recognition of *lingulata* as a distinct species. *Biloba* and *australis* are subspecies of one species on morphological, geographical, and genetical grounds. *Brandegeae* is morphologically and geographically a subspecies of this same species, although the reduction in fertility of the hybrids suggests an appreciable barrier to gene exchange. We have evidence, however, to suggest that this reduction in fertility is probably due to a single structural rearrangement of the chromosomes (Roberts and Lewis, 1955; Lewis and Roberts, 1956). Consequently, we have recognized *brandegeae*, *biloba*, and *australis* as subspecies of one species, *C. biloba* (Lewis and Lewis, 1955).

Cytological examination of meiosis in the *F₁* hybrids and a study of subsequent generations has given us additional information concerning the relationship and origin of some of these taxa but has made no further contribution to formal taxonomy. It has, however, answered such interesting questions as why the *F₁* hybrid *brandegeae x lingulata* is more fertile than *australis x lingulata*, despite the fact that all other evidence indicates that the relationship between the latter two taxa is much closer than between the former. The answer lies, paradoxically, in the fact that the

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chromosomes of *brandegeae* are structurally more different from *lingulata* than are those of *australis* (Lewis and Roberts, 1956).

Subspecies were found in the last example. To judge from an examination of recent monographs, subspecies (often ambiguously designated as varieties) are infrequent among flowering plants as compared, for example, with the vertebrates. Closely related taxa that replace one another so graphically are frequently found among flowering plants although these often prove to be distinct species, as was true of *Trichostema lanatum* and *T. parishii*, mentioned earlier. But such examples serve to indicate that geographical speciation, which has been so thoroughly considered by Professor Mayr (1942), is a common phenomenon among flowering plants. But if so, where are the subspecies? They do occur, of course, as we have seen in *Clarkia biloba* and as has been described in *Potentilla glandulosa* by the Carnegie group (Clausen, Keck, and Hiesey, 1940). The apparent infrequency of subspecies in flowering plants assuredly lies primarily in the inability of the plant taxonomist to recognize them. The principal limitation, of course, is the degree to which plants are modified by the environment in which they occur. A species of *Clarkia* may, for example, have flowers that are usually about 5 cm. in diameter, but one can also find depauperate individuals or even entire populations with flowers no more than 1 cm. in diameter (Lewis, 1953a). The seeds of these small-flowered plants have been shown to produce progenies under cultivation with the usual large flowers. Furthermore, the normally conspicuous differences between two species of California poppies (*Eschscholtzia*), are sometimes obscured by environmental modification (Lewis and Snow, 1951). If the differences between demonstrably valid species can be obscured by environmental modification, it is little wonder that many genetically determined infraspecific differences may not be readily perceived except under special conditions as, for example, when samples are grown under uniform cultural conditions. Many species under such conditions do show geographical differentiation in a number of traits such as rate of growth, time of flowering, branching habit, mature height, and the size of various organs. But when racial differences can be ascertained only under conditions of uniform culture, the question arises as to the purpose that would be served by describing them formally as subspecies.

A clear distinction should be made between the desirability of ascertaining and carefully documenting phenotypic differences that can only be shown by special techniques and the desirability of attempting to indicate these differences by a formal taxonomy. It would be sheer folly, I believe, to attempt to apply a formal taxonomy to the many phenotypic discontinuities that can be shown only with the use of special techniques. In this category I include not only the differences in morphology and physiological response that appear between populations under uniform and particular cultural conditions, but also those instances in which populations that are indistinguishable in external morphology are separated by strong internal barriers to gene exchange. To mention a few examples, in *Clarkia* most morphologically comparable populations with structurally and quantitatively similar genomes are completely interfertile, as one might expect, but the F₁ hybrids between other equally similar populations may be highly sterile and in other instances cannot be produced (Lewis, 1953a). In *Delphinium*, diploid races may be indistinguishable from their autotetraploid derivatives, except in chromosome number (Lewis and Epling, 1954). In *Holocarpha*, highly intersterile diploid races differ, apparently, only in the structure and number of chromosomes (Clausen, 1951).

The patterns of phenotypic differentiation are diverse among normally outcrossing diploid plants, as we have seen. But these patterns may be substantially complicated by agamic reproduction, self-pollination, and sometimes by polyplody. The results are appropriately called complexes. The designation of taxonomic categories in such complexes becomes one of convenience of reference, and each case presents a special taxonomic problem. The species and subspecies in these groups are, as has frequently been pointed out, comparable only by analogy to those in crossbreeding groups (see, for example, Stebbins, 1950).

In conclusion, perhaps we can risk a few summary statements, bearing in mind the limitations of such generalizations.

1. The pattern of morphological differentiation may differ from one group of plants to another and is a reflection of the diversity of evolutionary processes. Consequently, species and subspecies are not necessarily equivalent in different genera or different sections of the same genus.
2. Among sexually reproducing, normally outcrossing plants, the modern plant taxonomist recognizes as species morphologically delimit-
able groups separated by demonstrable or reasonably inferred barriers to gene exchange, although these, by no means need to be absolute.

3 The taxonomist recognizes as subspecies morphologically delimited geographical races between which an appreciable amount of gene exchange apparently occurs or, by inference, would occur were they to come in contact. But in flowering plants geographically expressed morphological differences of a magnitude to be evident, despite modification by the environment, are very often associated with barriers to gene exchange indicative of distinct species.

4 A distinction should be made between the desirability of ascertaining and recording phenotypic and genetic discontinuities, and their formal taxonomic recognition. When no purpose is served, formal taxonomic recognition should not be given to morphologically indistinguishable but reproductively isolated groups, nor to groups whose phenotypic discontinuity is evident only by special techniques.

5 Agamic and certain other complexes pose special taxonomic problems.

6 From an operational standpoint, a taxonomist considers such data as are available to him concerning all aspects of his material and then draws the taxonomic conclusions that seem to him to serve best the dual purpose of classification on the one hand, and an indication of genetic relationship on the other.

**QUESTION:**

What evolutionary significance do you attribute to introgression?

**DR. LEWIS:**

The process of evolution and the significance of the various factors contributing to it are a very different subject from the one we have been discussing, and one with which we might occupy ourselves all day. Briefly, the effect of introgression is to increase variation in the populations concerned. The evolutionary significance of increasing variation, and hence of introgression, depends upon a number of factors, which we could scarcely begin to discuss in the few remaining minutes.

**DR. SELANDER:**

Will you please give your conclusions as to the phylogeny of the species and races [of the genus *Clarkia*] used in illustrating your discussion?

**DR. LEWIS:**

Genomes with 9 chromosomes (*C. lingulata* and *C. dudleyana*) have in this instance been derived from genomes of 8 by the addition of a chromosome. *Clarkia lingulata* has been derived, we believe, directly from *C. biloba australis*, probably within relatively recent time (Lewis and Roberts, 1956). *Clarkia dudleyana* is probably not directly related to either of the other two species. To consider its phylogenetic relationship required the introduction of species that I have not mentioned. The subspecies of *C. biloba* that most closely approaches the ancestral race of that species would be difficult to determine. I suspect that *brandegeae* is most nearly ancestral, followed in sequence by *biloba* and *australis*, but I will not take the time to give you my reasons. A published account of these relationships is available (Lewis and Roberts, 1956).

**QUESTION:**

You have been dealing here with species and races of very limited distribution; other plants have a very wide distribution. Is there any indication that those with very limited distributions are specially adapted in such a way that they are confined by this adaptation to a particular area?

**DR. LEWIS:**

My examples have had a restricted distribution in the sense that they are confined to California. They were, in fact, chosen for study because they could be studied in their natural habitats throughout their range. However, a distribution restricted to 150 miles along the Sierra Nevada and 30 miles in depth is restricted only in terms of area. Within this area one has a rainfall gradient from north to south, elevational differences of 5,000 feet or more from east to west, and a multitude of edaphic differences. The environments within this area may far exceed those encountered by a species occupying a much larger area in an environmentally more uniform region. At the same time, one species does not occupy all of the diverse habitats in the Sierra Nevada within the area outlined by its limits of distribution.

The species of *Clarkia* are differentiated ecologically and show a very interesting correlation between phylogeny and habitat preference. The diploid species with the original basic chromosome number of 7 occupy, in general, the more mesic, older habitats, whereas those with derived basic numbers occupy drier, more recent, habitats (Lewis, 1953b). The basis of this adaptation to drier sites is not known nor do we know the extent to which races and species of *Clarkia* are specifically adapted to particular habitats. We have,
however, initiated experiments in which populations of several species have been established in diverse natural habitats outside of their natural range. The results of these experiments should help us to answer your question.

**QUESTION:**

My question is one of technique. You indicated in one example that two species may differ by characters that individually may overlap in variation but that do not overlap in combination. How are these characters measured and how are they combined in order to indicate a discontinuity?

**DR. LEWIS:**

The initial measurements differ with the trait to be measured. Linear measurements such as length are recorded in millimeters or other convenient units. Differences in other traits, such as the degree of glaucousness, can be scored subjectively by establishing a series of arbitrary classes, with the number of classes determined by convenience, and the nature of the variation. In order to combine such diverse measurements we have followed the method used by Edgar Anderson (1949) to construct hybrid indices, although in the example I gave no evidence of hybridization was found. The method consists of providing a common basis for all measurements by dividing the total variation of each trait into a convenient number of classes numbered in such a way that the combined results are additive. For example, A may have leaves that are longer, on the average, than those of B, but the internodes of A may be shorter, on the average, than those of B. To combine these traits we might assign a value of 1 to the shortest class of leaves and 10 to the longest. But for the internodes, the longest class would be scored 1 and the shortest 10. Assuming that one is combining 5 traits with the measurements of each divided into 10 classes, the total score for any individual would fall between 5 and 50. If these values were applied to the *Clarkia* example, that initiated the question, the scores for one species might fall between 5 and 25 and for the other between 35 and 50, with no scores between 25 and 35. This would then provide a graphic demonstration of the discontinuity that in this instance was perceived initially. But that, of course, was the reason the measurements were made.

**LITERATURE CITED**


### Specific and Infraspecific Categories in Microorganisms

**R. Y. STANIER**

I hope that my fellow-speakers and the members of the audience are not expecting to hear definitive answers from me. My plan is rather to raise a number of questions that seem relevant to the decision as to whether the species concept—or—perhaps better, a species concept—can be meaningful in the microbial realm. I shall restate my discussion to one small group, the unicellular true bacteria. The desirability of such a limitation becomes evident when one realizes that in the microbial world as a whole—algae, fungi, protozoa, and bacteria—we deal with a group of organisms that shows great diversity in sexual mechanisms, life cycles, modes of cellular construction, physi-
ology, and ecology. In fact, the biological divergences in the microbial world are so wide—much wider, really, than those that separate higher plants and animals—that meaningful species concepts, if and when they are developed, may very well be singular concepts, each valid only in the context of a particular microbial group.

I should like to start out by giving you a brief account of the salient biological properties of unicellular true bacteria. These organisms reproduce in very large part, and often exclusively, by binary fission. It is probable that most of them are haploid throughout almost the entire life cycle. In fact, the only bacterium about which we can make this statement with certainty is Escherichia coli, where the genetic evidence for the predominance of the haplophase is quite conclusive. However, since the rates of spontaneous and induced mutations in many other bacteria are of the same order of magnitude as those observed in E. coli, it is plausible to infer that haploidy is widespread. Hence mutational events in bacteria will be immediately expressed, and selection will press hard on bacterial populations. There would appear to be no possibility of building up a masked store of genetic diversity within a bacterial population.

Populations of bacteria have two properties which will appear unfamiliar to those accustomed to think in terms of populations of higher organisms. One is their very large sizes. To give a trivial example, there are probably more representatives of the bacterial type known as Streptococcus fecalis in the intestinal tract of any given mammal than there are representatives of that mammalian species in the entire world. This factor of population size, coupled with rapid population turnover, no doubt compensates in part for the inability of bacteria to maintain a reservoir of genetic diversity masked by dominance, since a wide variety of spontaneous mutations must be arising in the population at all times. A second distinguishing feature of bacterial populations is their capacity for dormancy. This is seen most strikingly in spore-forming bacteria: the spores of species whose vegetative generation time is only 30 minutes can persist in viable condition for as long as 50 years. This is an extreme case; but even in nonspore-forming bacteria the vegetative cells can remain viable in a nongrowing state for periods that are extremely long compared to the generation time.

Let us now turn to the existence and nature of mechanisms of gene transfer in bacteria. Bacterial genetics is a relatively new field of study, and as far as gene transfer is concerned we are quite evidently only at the beginning of the learning process. But even on the basis of our present meager knowledge, it is already established that some bacteria possess highly specialized and unorthodox mechanisms for effecting gene transfers.

Let us consider first the one perhaps more or less orthodox case: recombination as studied by Lederberg and others (Lederberg, 1955), in Escherichia coli. As originally described by Lederberg and Tatum (1946) and by Lederberg (1947), recombination in E. coli appeared to be relatively simple and straightforward. This bacterium could be described, on the basis of their work, as an organism in which the haplophase was predominant and in which zygote formation occurred, without distinction of mating type, at rather rare intervals in vegetative populations, to be followed immediately by reduction division to yield haploid progeny again. In the past three years, the picture has become considerably more complex. In the first place, the existence of a mating type system has been established; and one, furthermore, with a very striking and interesting peculiarity. Mating type specificity is infectively transmissible in one direction, such transfer of mating type specificity being quite separate from an act of genetic recombination. Furthermore, it has become evident, particularly in the first instance from the work of Hayes (1952) that a considerable number of genes carried by the parent of the so-called F+ type fail to get through the cross, a fact which could be interpreted either as reflecting post-zygotic elimination (Lederberg, 1955); or as the failure of part of the F+ genetic complement to get into the cross (Watson and Hayes, 1953). On the whole the evidence seems to favor the former interpretation. Lastly, there are the very interesting recent experiments of Wollman and Jacob (1955), which show that the genetic transfer during mating from the F+ to the F− cell is a gradual process, which can be interrupted mechanically during its course, to give rise to partial recombinants: to use a crude analogy, it appears as if the F+ genome were insinuating its way into the F− cell like a piece of spaghetti, which can be chopped off at any given moment during its entry by mechanical interruption. Consequently, even the most nearly orthodox mechanism of gene transfer known in bacteria has some highly unusual features about it, and it is not yet by any
means certain that recombination in E. coli can be fitted into classical genetic patterns.

From this, we go to other bacterial mechanisms of gene transfer which have no analogies in any other biological group. The first of these is the phenomenon of transduction, originally discovered by Zinder and Lederberg (1952) in the Salmonella group, which is related to E. coli, and more recently demonstrated in certain strains of E. coli (Lennox, 1955; Jacob, 1955). Transduction is a unidirectional transfer, involving one or a few genes, and the transfer of any given character occurs with a relatively low frequency. It is mediated by an infecting particle of a bacterial virus, derived from the donor parent and entering the receptor parent, with which it establishes a so-called lysogenic relationship, its genome becoming closely integrated with the genetic structure of the receptor cell. As an apparently more or less incidental event, such a virus particle may carry over part of the genome of the bacterial cell from which it comes. In principle, transduction would appear to be a possible mechanism of gene transfer in any bacterial group where lysogenic viruses occur; hence it may well be a fairly widespread phenomenon among bacteria. Another kind of modification of host properties which accompanies the establishment of a lysogenic relationship, apparently different from transduction, has been described recently in the diphtheria bacillus, Corynebacterium diphtheriae (Freeman, 1951; Barksdale and Pappenheimer, 1954). It has been established that all toxin-producing strains of C. diphtheriae are lysogenic, and that the particular bacterial virus concerned will confer the capacity for toxin production (and hence for virulence) on other, non-toxin-producing, avirulent strains of the species by lysogenization. In marked contrast to the Salmonella situation, there is nothing random about the transfer of toxin-producing capacity: every lysogenized bacterial cell of an avirulent strain acquires toxigenicity and virulence upon lysogenization. In this case, one may perhaps imagine that the gene for toxin production by C. diphtheriae is also a necessary genetic component of the bacterial virus itself. Indeed, the work of the past few years on the phenomenon of lysogeny (see Lwoff, 1953, for a general account) has suggested that the genetic systems of bacteria and bacterial viruses are very closely related, since the viral genome is capable under conditions of lysogenization of becoming smoothly incorporated with that of the host.

The last mechanism of gene transfer in bacteria, which occurs in the Pneumococcus and in the Hemophilus group, is known as transformation [see Hotchkiss (1955) for a review]. Desoxyribonucleic acid extracted from cells of one genotype can, when applied to cells of a different genotype, cause the permanent acquisition of properties characteristic of the first strain. The transformations have a certain similarity to the transductions. In both cases, only one or a very small number of determinants are transferred in any single act, and the probability of transferring any given character is very small. On the present evidence, there seems to be a certain complementarity between transformability and transductability: virus infections of the transformable bacteria do not seem to exist, and transformations have never been described in those forms where transduction is known. One could perhaps imagine that transformable bacteria are those that can absorb free DNA through the cell membrane, and incorporate it into their genetic complement, whereas transducible ones need to have it sugar-coated in the form of a virus protein envelope, which serves as a vehicle for entry into the cell.

As I am sure you will all realize, it is difficult at present to assess the evolutionary and taxonomic significance of these methods of bacterial gene transfer. It seems improbable, however, that they have much importance in bacterial evolutionary dynamics, if the inference that haploidy predominates is correct; in haploid populations, the immediacy of selection will severely limit the amount of variation that exists, and leave nothing much worth transferring from one member to another.

To conclude this rapid survey of the biology of bacteria, I should like to discuss briefly the problems of bacterial ecology, which again have few resemblances to the problems encountered by ecologists who study higher organisms. In the first place, we know that there are no geographical limitations on the distribution of bacteria except in the case of pathogenic forms, whose ranges are of course delimited by the ranges of their hosts. Instead, when we think about bacterial ecology, we are forced to think in terms of micro-environments. In the soil, for example, a single fiber of cellulose a few hundred cubic microns in volume will provide the site for the development of a number of very highly specialized microbial forms. Such micro-environments, of which there may be thousands, each one clearly distinct from the rest, in a few grams of soil, can occur in any
part of the world, a fact that explains the lack of geographical limitations on bacterial distribution. Microbiologists possess a very powerful tool for the study of this kind of physico-chemical microbiology: the enrichment culture. One prepares an artificial environment in the form of a culture medium whose exact chemical composition is known, inoculates it with a gram of soil, and incubates it under rigidly prescribed conditions. As a rule, one gets the exclusive primary development of a particular microbial type, and since the environment has been pre-specified one can then say with considerable precision what the physico-chemical conditions that lead to abundant development of this particular form will be. I should like to illustrate the ecological insights which can be achieved by enrichment culture methods by considering one example, the group of aerobic nitrogen-fixing bacteria known as the *Azotobacter* group. The members of this group, found in fertile soils all over the world, can be enriched for, even when they constitute a very minor component of the soil microflora, by preparing a medium with a suitable energy source but devoid of combined nitrogen, inoculating it with soil, and incubating under aerobic conditions. *Azotobacter*, if present in the soil, will invariably develop as the exclusive primary population. When the nitrogen requirements of the organisms are tested with pure cultures, one finds that they grow somewhat better at the expense of ammonia or nitrate than at the expense of atmospheric nitrogen. From this, it might be imagined that a successful enrichment culture could be obtained by adding ammonia or nitrate to the medium; but experiment shows that in such an enrichment medium with combined nitrogen, *Azotobacter* never comes to the fore, and even though the cells are highly characteristic, it is not even detectable microscopically as a component of the primary microflora. Such an experiment therefore shows that the capacity to fix atmospheric nitrogen is an essential one for the survival of the group in nature, even though it may be dispensable under the highly artificial conditions of pure cultivation, where an organism is removed from the influence of all biological selective pressures. The insights provided by enrichment culture experiments also frequently help a great deal in the selection of taxonomic characters. Thus, in the case of the *Azotobacter* group the capacity for nitrogen fixation is actually a very important taxonomic group character; and even if it proved to be a genetically unstable character in pure cultures, we should still be justified in using it on the basis of our knowledge that under conditions of free biological competition it is certain to be preserved in *Azotobacter* populations by selection.

From what has been said in the foregoing paragraphs, I am sure that it will be evident to you that the bacteria are utterly distinct in their life cycle, modes of gene transfer, population dynamics, and ecology from the higher plants and animals. Consequently, it is unnecessary to consider whether the species concepts which were outlined so admirably this morning by Professor Mayr are applicable to bacteria: they are simply irrelevant in this particular frame of biological discourse. The question which the bacteriologist (and other microbiologists as well) must ask himself is, rather, whether there is any other fashion of defining an ultimate taxonomic unit for organisms with the particular constellation of biological properties that he encounters. In fact, I believe that very few bacteriologists have consciously asked themselves this question, despite the fact that they blithely employ binomial designations and thereby implicitly affirm their belief in the reality of the bacterial species. Is this simply a blind adherence to biological tradition? Probably not. The entities to which we give binomial designations in bacteriology are meaningful, in the sense that when I say "*Escherichia coli*" to another bacteriologist, it conveys a certain Gestalt to him, which I intended to convey, and which is different from what I would have conveyed by saying "*Escherichia freundii*." So far, however, an abstract definition of the kind of difference implicit in such usage has not been produced. This leads me to believe that the species concepts of the botanist and zoologist are not the only members of a conceptual class, and that perhaps in the end we shall find other, quite different ways of defining basic taxonomic units in the microbial world, valid only for these particular biological groups.

Whether or not the attempt to formulate such new species concepts is worthwhile depends on the way in which variation is distributed through related clonal bundles in bacteria and other microorganisms. Do there exist in nature groups of bacterial clones sharply distinguished from the nearest related clonal bundles by multiple phenotypic differences, or is the pattern of variation reticulate? If the latter situation obtains, there is not much use in trying to search for a definition of the species; but if we do, in fact, find multiple discontinuities between related clonal bundles, then we have a right to enquire about the evol-
tory dynamics which might be responsible for bringing about and perpetuating this situation.

In evaluating taxonomic work with bacteria, the question of taxonomic method is paramount, although the inherent methodological difficulties have been ignored by most practising bacteriologists. It is a truism imparted to students in every elementary bacteriology course that one identifies bacteria by what they do rather than by what they look like. The easily ascertainable morphological features of bacteria are so few in number that they are at best useful in distinguishing families or higher taxonomic categories. For the purposes of a finer taxonomic resolution we must depend on physiological and biochemical properties to an extent unknown in other biological groups, except possibly the yeasts. And this is precisely the place at which the main difficulty of bacterial taxonomy—largely unrecognized by bacteriologists—comes in. In order to find out about the physiology or biochemistry of an organism we have to perform experiments. We can, therefore, ask the organism $n$ different questions by placing it in $n$ different experimental situations, $n$ being a very large number indeed. However, of the $n$ specific answers that we could obtain, only a very small fraction will be of any value taxonomically; and since our time and patience have limits, it is entirely conceivable that we may fail to perform precisely those experiments which would have given us taxonomically valuable answers. A good analogy is the difficulty that would face a color-blind man asked to classify a collection of green and red balls. Since he could not see the color difference, the only way in which he could go about the operation would be to classify by size, whereas if he had had normal color vision he could have divided this group of objects into two mutually exclusive categories at first glance. The bacteriologist is precisely in the position of the color-blind man. He often has no way of knowing a priori what particular experiments, or indeed how many experiments, he should carry out in order to obtain the indispensable minimum of taxonomically useful information. For this reason, a large part of the work done on the taxonomy of bacteria gives us little indication about the true relations that might exist in the objects studied. Many bacteriologists simply take an arbitrary set of 15 or 20 differential tests and apply them to a large number of strains, after which they are reduced to making analyses of frequency distributions in an attempt to draw lines through a hopeless reticulate pattern of variation. An example of this taxonomic approach, often cited as a classical piece of bacterial taxonomy, is the study by the Winslows (1908) of the systematic relationships of the Coccaceae, a study which led them to conclude that bacterial species can be segregated only by a statistical analysis of the frequency distributions of characters. This work is particularly interesting as an illustration of faulty taxonomic method, because subsequent studies on some of the bacteria investigated by the Winslows have revealed the taxonomically significant properties which the Winslows failed to discover. Thus we cannot always accept claims for a reticulate pattern of variation in bacteria at their face value; they may be fallacious, based on faulty taxonomic method.

There are a few bacterial groups where taxonomic studies conducted with care and biological insight have clearly revealed the existence of very marked multiple discontinuities between related clonal bundles. Perhaps the best of these is the study of a particular group of photosynthetic bacteria, the non-sulfur purple bacteria, by van Niel (1944). These forms can all be isolated by simple and clearly defined enrichment methods. In taxonomizing the group, van Niel started out by making a very careful study of their ecology through the application of slight modifications of the basic group enrichment procedure, until eventually he was able to isolate at will any given member of the group by utilizing a special modification of the general enrichment procedure. The information obtained by this ecological study proved in the end to be the key to a satisfactory taxonomic arrangement; in other words, some of the taxonomically significant properties were already revealed by the enrichment procedures. Working with several hundred strains, van Niel was eventually able to divide them into six fundamental clonal groups, which he designated as six species. So clear were the distinctions between these species, that he was able to construct three sets of determinative keys, based respectively on morphological, physiological, and biochemical properties, any one of which would serve to make a specific identification. One particular physiological feature of the group not studied by van Niel was the vitamin requirements. A later investigation of this matter by Hutner (1950) revealed the striking fact that van Niel's species were also characterized by specific constellations of vitamin requirements. In fact, one could also identify an unknown strain with one of the established species by determining its vitamin requirements, with little chance of error. Hence in this bacterial
group, it is quite evident that there are sharp and multiple discontinuities between related groups of clones, a fact which permits the establishment of specific entities that are entirely satisfactory from a practical standpoint, and that evidently correspond to a series of distinct ecotypes. In a few other bacterial groups the same kind of situation has been shown to exist, and I believe the development of adequate taxonomic methods—with bacteria, each group imposes its own special methodology—would reveal the existence of many more. As yet, however, we have no clues as to the evolutionary mechanisms responsible.

Dr. Mayr:

I must say that what interested me most was the fact I had only a very vague knowledge of the existence of these very definite bundles in certain groups of bacteria. What about E. coli and Salmonella—is there almost a complete intergradation between extreme types in species as sometimes claimed?

Dr. Stanier:

Well, the Salmonella group is a special case, because here bacteriologists who are Salmonella specialists have developed a very refined method of antigenic analysis which essentially enables them to discriminate between single gene differences that are expressed structurally in the outer membrane of the bacterium. I feel that within the Salmonella group the classification which the bacteriologists have adopted is a classification based on single gene differences and hence that what they call taxonomic units are really nothing of the sort. They are minor variations in large populations.

Dr. Mayr:

What is known about the ultimate history of some of the nuclei that enter the central carriers in the things Pontecorvo worked with? Are they always heterocaryotic or do they only contain one type?

Dr. Stanier:

I don’t know about the natural occurrence of heterocaryosis. It has not really been extensively studied. But if you are playing with artificial heterocaryons you can maneuver them by environmental pressures until they contain one kind of nucleus or the other kind or a balanced mixture of the two. This is the really fascinating genetic part of this situation; by manipulating the environment you can play on a sort of natural selection inside the cell for different nuclear types.

Dr. Mayr:

I believe that there are no further questions; it is time now for a short intermission.

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Specific and Infraspecific Categories in Fossil Mammals

R. A. STIRTON

Colloquiums like this one are attempts to disclose the point of view of the individual as based on his concepts and reasoning. Time and critical observations will test the validity of his ideas. The research that I have attempted in the recognition of specific and infraspecific categories in some species of fossil mammals is still in progress, but I shall attempt to give you my reactions on the subject at this time.

Much has been written on species and subspecies problems in the past thirty years. This has been of mutual benefit to geneticists, neontologists, and paleontologists and has tended to bring investigators nearer to a consensus in approaching these problems. But more critical, well documented work must be done in paleontology for a better understanding of these taxonomic categories as they are applied to fossil remains. Though paleontologists have used the binomial system for more than 150 years, a species concept was not always clear in their minds, nor was it necessarily their objective when a species name was proposed. With limited materials at hand—frequently a tooth, part of a jaw, a skull, or rarely most of a skeleton—each investigator formulated his own ideas of a species as expressed in the phenotypic characters before him. Of course many synonyms were erected, but on the other hand, many of these earlier workers seemed to have a rather keen appreciation of species as proved by subsequent discoveries. It is true that a great number of our so-called species still listed in the fossil record will eventually be recognized as genera; nevertheless, some species represented by adequate samples with good evidence of contemporaneity in the local population samples are equivalent in rank to some neontologic species. Most of these extinct species are in need of revision as based on additional specimens with stratigraphic or phyletic control. I know of no extinct species of mammal as fully represented by subspecies populations as most species of living mammals. If equivalent materials were available in the fossil record it would be extremely doubtful that contemporaneity for all of the samples for a span of as much as 200,000 years could be established. This is because of the nature of the deposition and redeposition of sediments, and our inability to determine the length of time involved in the deposition of sedimentary units, as well as the duration of time breaks between stratigraphic units.

In the Great Plains region and elsewhere, the evidence of superposition in continental beds in adjacent areas is at times difficult to determine because of the intermittent deposition and channeling effects of stream and flood plain deposits. Frequently, under these conditions fossils are washed out and redeposited with the remains of animals of a later age, but the redeposited fossils usually can be detected because of their small number or by the effect of abrasion on them, and hence are seldom confusing in a correlation of the beds. Sometimes a few feet of down cutting over a wide alluvial plane can be quite confusing in determining the superposition of adjacent exposures. In some areas the overlying later deposits and the soil mantle make it almost impossible to trace stratigraphic units from one exposure to another. This becomes particularly confusing when the lithology is the same in an area where volcanic materials of the same composition have come from the same or different local sources at slightly different times, or where the same lithic materials have been reworked and secondarily deposited. This is well demonstrated in some Pliocene formations in the San Francisco Bay region where we have had to use the evidence from fossil mammals to correlate the stratigraphic units in which they occur.

Periods of heavy rainfall accompanied by local subsidence may result in a thick accumulation of sediments in a relatively short time. This is exemplified in the Ventura Basin, California, where about 8,000 feet of sediments have been laid down since the inception of glaciation in the late Pliocene. In other places, as indicated by the fossil remains, less than 100 feet of sands and clays were deposited at the same time. The stratigrapher must rely on the morphologic features in fossils, either in the identity of species, or in the stage of evolution in the organisms, to be assured of a more precise dating of a given rock unit.

Frequently it is difficult, if not impossible, to know without fossils even in superimposed stratigraphic units, whether an erosional unconformity is indicative of a temporary break in deposition or represents removal or nondeposition in that area from one to five million years. Stratigraphic and lithologic evidence in correlation, then, must be used with caution.
Change in local environment during deposition of flood plain sediments with apparent subspecies chronocline.
The trinomial was introduced into Tertiary mammalian taxonomy by E. D. Cope in his “Synopsis of the Oreoontidae” in 1884. In three genera he listed five species and eleven subspecies. Cope apparently was influenced by the work of F. W. True and others in their classifications of Recent mammals. Evidently Cope thought Cenozoic mammals would exemplify these same taxonomic categories. The type concept instead of the population concept of a species was invoked at that time and prevailed for over fifty years when J. C. Merriam (1906), W. J. Sinclair (1905), Barnum Brown (1908), W. D. Matthew and H. J. Cook (1909), and others named subspecies. Minor morphological differences in examples were generally considered to be indicative of subspecies, and characters of slightly greater magnitude were the clue to species. Frequently two subspecies were named from one quarry, from the same cave breccia, or from a widespread flood plain horizon, which in modern methods we usually think of as evidence for our closest approach to contemporaneity in the fossil record.

These early named paleosubspecies for the most part have not been reviewed as population samples thus using the modern approach to these problems, though some investigators are attempting to recognize subspecies on other samples more recently collected. Indeed some paleomammalogists continue to propose subspecies much in the same manner with little or no reference to time and space controls.

In a recent series of papers constituting the revision of an extinct family of Tertiary mammals (12 genera, 25 species, and 61 subspecies are recognized. The materials are excellent for fossil mammals, usually representing complete crania and mandibles with samples ranging from one to more than one hundred individuals. Frequently two subspecies are recorded from the same fossil assemblage or from one quarry. Both geographic and geologic subspecies are recorded. Though these are herbivorous animals of medium to large size, the trinomial has been applied to so-called geographic varieties with samples sometimes less than 100 miles apart in an area where there was little geographic relief at the time the animals lived, a situation quite unlikely to effect isolation. Likewise vertical or time stratigraphic controls are assumed or not mentioned. That detailed information on the stratigraphy may appear in future reports on the subject is of little satisfaction to the reader who is attempting to determine the validity of these infraspecific categories. Without going into a full critique I may say that these authors have not demonstrated proof from their observations for their contention that these are subspecies. This can be considered as an extreme example not practised nor approved by most mammalian paleontologists.

There is little doubt that the processes of speciation in mammals during the Cenozoic happened much as we see it today in Recent animals. Changes in topography may have accelerated speciation and evolution both locally and regionally, but it is doubtful that these influences were so profound, across what is now temperate North America, during most of the Tertiary as they were in the late Pliocene, Pleistocene, and Recent. Though there was a gradual change from warm moist to cool dry climates from northern to southern latitudes in the Tertiary, our evidence of orogenies has led me to the conclusion that life zones and climatic conditions at any given time during that period were, on the whole, more uniform and of wider extent than today. There were uplifts in the earth’s crust at different times and in different areas, but they were not of the magnitude of the diastrophic disturbances at the close of the Cenozoic which are still in process. Therefore I should not expect the subspecies patterns at any given time from the beginning of the Puer- can (early Paleocene) to the initiation of the epi- rogeny at the close of the Hemphillian (middle Pliocene) to be as complex as they are today. We may have wide ranging subspecies populations of medium to large mammals represented in a vertical succession of sedimentary rocks showing intergradation in a chronocline. Thus a 400-600 mile drift in populations within a score or more years could represent only local populations of a subspecies. There is some suggestion of this in Miocene and Pliocene faunas east of the Rocky Mountain region. The difficulty here would be in determining whether the characters were of specific or of subspecific magnitude. The fossil collections of small mammals, though increasing rapidly, are still too incomplete, except in a few cases, to adequately exemplify subspecies phenomena. Indeed in most instances one is hard pressed to be satisfied with specific identifications.

It is desirable and useful to classify fossils in the same taxonomic framework used for Recent animals, as best we can, since the Recent animals are the present product of an evolutionary process that also required time. A subspecies to include a paleontologic concept, might be defined as: geographically and/or stratigraphically defined.
aggregates of local populations which differ morphologically from other such subdivisions of a species (modified from Mayr, Linsley, and Usinger, 1953). The genetic constitution and the degree of reproductive isolation can only be inferred from the morphologic characters, the geographic location, and the stratigraphic position of the fossil samples.

A thorough critical analysis of detailed data might, in certain samples, reveal subspecies in the Tertiary fossil record particularly in a vertical sequence in a continuous stratigraphic section; but it will be almost impossible to differentiate between subspecies populations that were successful in phyletic evolution in a given area from a closely related subspecies from elsewhere that has invaded the area because of a change in the local environment. An example of this kind can be readily visualized (Figure 5) in a pattern of divergent speciation when an adaptive subzone B (the vertical section of the sample) is altered to the degree that it has become more like an adjacent adaptive subzone C. In this instance the populations of subspecies B would become extinct or disperse elsewhere while the better adapted subspecies C would immediately spread into area B. Though subspecies B could interbreed with subspecies C, it was now too far removed physiologically from subspecies C to tolerate the environment of that subspecies. This pattern would be more typical of small mammals like squirrels, mice, and shrews. This is quite possible because nothing is static nor fixed in trend in evolution. The environment evolves as well as the organisms that help make up that environment. Thus the animals represented in any series of locally superimposed beds could include subspecies or even distinct species of two chronoclines not distinguishable by morphologic characters.

Paleontologists are not only encumbered by necessity of inference of the genetic constitution and of the reproductive isolation in their attempts to recognize subspecies, but the nature of the materials limits their observations. Neomammalogists utilize texture and color of pelage, overall measurements (total length, length of tail, etc.), as well as habits and mannerisms, which are not available to paleontologists. Adequate samples of complete crania are seldom found. Complete or partial dental series, and more frequently isolated teeth are the usual samples.

In 1943 Simpson directed attention to the analogy of clines as proposed by Huxley (1938) and the continuous vertical sequences of paleontologists are not only encumbered by necessity of inference of the genetic constitution and of the reproductive isolation in their attempts to recognize subspecies, but the nature of the materials limits their observations. Neomammalogists utilize texture and color of pelage, overall measurements (total length, length of tail, etc.), as well as habits and mannerisms, which are not available to paleontologists. Adequate samples of complete crania are seldom found. Complete or partial dental series, and more frequently isolated teeth are the usual samples.

In 1943 Simpson directed attention to the analogy of clines as proposed by Huxley (1938) and the continuous vertical sequences of paleon-

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2 As a matter of fact such samples do exist in one collection, but unfortunately they are seen by very few people.
COLUMNAR SECTION IN LA VENTA BADLANDS.

- Upper Red Bed.
- Unit Between Fish Bed & Yellow Sands.
- Monkey Unit.
- Cerbatana Gravels & Clays.
- El Libano Sands & Clays.

VERTICAL SCALE IN METERS

Figure 7
tology. Simpson then introduced the terms "choro-
clines" for the "space clines," and "chronoclines"2
for the "time clines." He exemplified a chrono-
cline by four "ascending stages" in a unit phylum
of the genus Ectocion, a genus of Condyarthra
from the late Paleocene and early Eocene of Wy-
oming. A subspecies of the species E. osbornianus
is recognized from each of the stratigraphic units.
Simpson's data were taken from a single variate,
the length of $M_1$, but he indicated that other vari-
ates in the same samples confirmed his conclusion.
There is a continuous gradation from 5.3-5.6 mm.
to 8.1-8.4 mm. in the lengths of these teeth from
the base to the top in this sequence (Clark Fork
samples do not overlap in every character, but
some of the samples, especially that from the Lost
Cabin, are very small and the populations almost
certainly did overlap. Even in Lost Cabin times
[highest in the sequence], there were undoubtedly
some Ectocions of this lineage that were as small
as some of the larger individual variants in the
long precedent Clark Fork [lowest in the se-
cquence] and that could indeed hardly be distin-
guished from the latter if they were compared as
individuals.”

If these are subspecies it is logical to assume
they represent ancestors to descendents in a suc-
cession of deposits in a given area. On the other
hand, as I have explained above, the area may
have been invaded by a subspecies of another
phyletic line from a contiguous area (see Figure
5). Furthermore the characters as given do not
exclude the possibility of their being of specific
magnitude. Comparable living species with over-
lapping characters are Peromyscus maniculatus
and P. leucopus, or Odocoileus hemionus and O.
virginianus. Many more could be cited. The rec-
ognition of the Ectocion samples as species is no
more artificial than calling them subspecies, since
in either case it is based on the author's interpre-
tation of the magnitude of the differences.

A few years ago University of California ex-
peditions to Colombia found rather abundant re-
 mains of an interathere, Miocochilius anomalopus
Stirton (1953), from the base to the top in a
stratigraphic section in the La Venta badlands, in
the upper Magdalena Valley. Our first discoveries
seemed to indicate a significant size difference in
the specimens in the lower El Libano unit from
those in the Monkey unit 700 meters higher in the
section. Here it could be assumed would be an
excellent opportunity to recognize subspecies in a
chrono-cline. Though no qualitative features were
apparent to demonstrate such an evolutionary
trend, it was thought that quantitative characters
in anteroposterior measurements in the cheektooth
series would be indicative. Measurements were
taken from $P_3-M_3$, $P_1-M_3$, $M_3-M_5$ and $P_3-P_4$, in
different series of measurements. From the
bottom to the top of the section, there were three
measurable samples from El Libano, seven to ten
from Cerbatana, seven to ten from the Monkey
unit, one between the Fish Bed and the Yellow
Sand, and one to three from the Upper Red Bed.
Scattergrams soon showed no consistent trend in
these measurements in specimens from the base
to the top of the section. Yet surely enough time
was involved in the deposition of these rocks for
subspecific if not specific evolution to have taken
place. Some of the thickest units in the section
were clays and fine sandy clays which normally
are deposited slowly. It should not be concluded
that the interatheres from the El Libano and those
from the Monkey unit were not good subspecies
as indicated by our measurements. They may have
possessed other differences not observable in the
fossils, but we could not recognize them.

Progressive hypsodonty in the populations of
Tertiary Equidae starting with an advanced spe-
cies of Parahippus in the early Miocene and cul-
minating in extremely high crowned teeth in sev-
eral phyletic lines demonstrates almost impercepti-
able intergradation from beginning to end. These
samples are currently listed as genera and species,
though some trinomials have been proposed by
Osborn (1918). It is not too difficult, to designate
arbitrarily certain species to be included in a
genus in a sequence of this kind, but knowledge
of the less distinct characters with stratigraphic
controls has not yet made it possible to differen-
tiate between species and advanced subspecies.

Frequently other characters together with a
slight increase in the height of crown of the
cheekteeth give us clues to relationships. I can ex-
emplify this best with two closely related species
of the equid genus Neohipparion, N. floresi Stir-
ton (1955), and N. arellanoi Stirton (1955),
from the middle Pliocene Boquilla formation in
the Rio Papigochic Valley, Chihuahua, Mexico.
These species show their nearest relationships to
Neohipparion eurystyle (Cope) from the Pan-
handle of Texas and Oklahoma, and are more
distantly related to Neohipparion phosphorum
(Simpson) from the Alachua fauna of Florida.
Miocochilius anomopodus Stirton, n. gen. and n. sp.

Length M₁₆ (lowers) in millimeters

Length P₁₆ (lowers) in millimeters

Figure 9
All are middle Pliocene, and are among the more progressive species of the genus. A large number of maxillary and mandibular cheekteeth series, isolated cheekteeth, and metapodials were available. The species were not found in the same assemblages or localities, but one species was found in 3 localities and the other in 3 different localities. It is interesting to note, however, that Mr. Lloyd C. Pray's studies on the stratigraphy offer no basis for a time difference between the assemblages from these localities.

An analysis of the diagnostic characters of the two proposed species may give a clearer idea of the magnitude of their differences (Figure 11).

The height of crown in the cheekteeth is difficult to determine in hypsodont equids, except in a few specimens, even in relatively large series, if the tooth is not worn, or sometimes when it is little worn, or if the base of the crown is not formed or is broken. If the base is well formed, the tooth is usually worn to a point where its total crown height is no longer determinable. In closely related species like these a slight difference in the standard range could be significant if accurate measurements of a series could be made.\(^3\) Though there is a variation in the crown height in different individuals, \emph{N. arellanoi} seems to average from 5 to 10 mm. lower crowned than \emph{N. floresi}. This character is only suggestive.

The anterior end of the lingual border of the prefossette on \(P^2\) extends farther forward than the anterolabial corner in 9 of 12 specimens of \emph{N.}.

\(^3\) This does not suggest that stage or age correlation based on hypsodonty is invalid. The studies here are of much greater refinement.

\begin{figure}
\centering
\includegraphics[width=\textwidth]{species_subspecies.png}
\caption{The species and subspecies measured are: mg—\emph{maniculatus gambelli}, mb—\emph{borealalis}, mc—\emph{clementis}, me—\emph{elasus}; lc—\emph{leucopus caudatus}, ll—\emph{leucopus}, ln—\emph{novoboracensis}, lt—\emph{tornillo}; gg—\emph{gossypinus gossypinus}, gp—\emph{palmarius}; tn—\emph{truei nevadensis}, tm—\emph{montipinoris}, tg—\emph{gilberti}, ts—\emph{sequoiensis}; ss—\emph{sitkensis sitkensis}, so—\emph{oceanicus}.}
\end{figure}
**Figure 11**

Floresi from localities 275 and 281. In the only three specimens of *N. arellanoi* from locality 276 the inner border is not farther than the anterolabial corner. Though the sample is small for both species the differences seem significant.

The inner edges of the protocones tend to be straighter in *N. floresi*, whereas in *N. arellanoi* they tend to be markedly concave. This feature is perhaps more variable than any other listed in the diagnosis. Frequently, it varies in different stages of wear and is difficult to evaluate.

The bifurcation of the anterior end of the protocone (fish-pattern) in the early stages of wear in M\(^3\) is one of the most consistent characters. It is seldom if ever present when the tooth first starts to wear nor is it present in the lower half of the crown. It is present in 17 specimens, or all of the specimens of *N. floresi* in early stages of wear from locality 275, and it is even present in two of the first or second molars. Of the 7 specimens of *N. arellanoi* from localities 276 and 289, one has the fishtail pattern and it is absent in the others. This could mark one of the first appearances of the character in a less progressive population or it could have been mixed in applying the field number as is indicated in another instance.

The lingual extension of the prefossette loop, though variable in its length, seems significant in the sample of *N. floresi* from locality 275, where 70 of 82 specimens show an extension beyond the lingual borders of the fossettes. On the other hand the sample of *N. arellanoi* from locality 289, though less extensive lingually, shows 11 of 27 individuals that project at least beyond the borders of the fossettes. The smaller sample of *N. arellanoi* is even more distinct from *N. floresi* in that only 2 out of 11 show a slight extension beyond the fossette borders.

The deciduous molars (DP\(^3\) to DP\(^4\)) of *N. floresi* show an anterolabial spur on the protocone in all of the five specimens in early stages of wear, and the fishtail pattern is developed on one. All of these are from locality 275. The 3 specimens of *N. arellanoi* from locality 276, two in early stages
of wear, show no spur and the protocone is sharply crescentic in outline, in contrast to a nearly straight lingual border in \textit{N. floresi}.

In the lower molar, $M_2$, \textit{N. floresi} is consistently shorter anteroposteriorly and shows less tendency to converge toward the top of the crown. In these teeth \textit{N. arellanoi} seems to be larger and shorter crowned. The mean averages of the samples of \textit{N. arellanoi} (24.5 mm.) are more than 3 mm. longer anteroposteriorly 20 mm.± above the base of the teeth than in \textit{N. floresi} (21.7) and there is no overlap in the measurements in the samples available, though I expect a larger sample would show a slight overlap.

The \textit{lingual fold in the metaconid-metastylid groove} in the lower premolars is a conspicuous character. Though it is variable in its intensity in \textit{N. floresi}, it is much more prominent than in \textit{N. arellanoi}, where it is absent or faintly indicated in early stages of wear. I have not been able to derive a quantitative value for this character, though it is very useful as a qualitative feature.

A survey of all of the features in the teeth and in the metapodials of \textit{N. floresi}, and \textit{N. arellanoi}, indicates a remarkably close relationship. Since there is an intergradation of varying degree in seven of the nine diagnostic characters, these forms might be interpreted as representing successive subspecies in a chronoline. Though characters are not necessarily of equivalent value in different species or subspecies, nevertheless, when similar dental features are compared in the horse, the ass, and the zebras, it is felt that the characters displayed in the Papigochic neohipparions are of at least equivalent if not of greater magnitude than in the living equids. Consequently I prefer to recognize the fossil forms as distinct species.

Good Pleistocene samples where adequate comparison can be made with living subspecies offer the best possibilities in recognizing subspecies in extinct mammals. The specimens must be in sufficient numbers and completeness of crania and mandibles to offer the necessary evidence.

Colbert and Hootje (1953) in their excellent report on the “Pleistocene Mammals from the Limestone Fissures of Szechwan, China,” based a subspecies of bamboo rats, \textit{Rhizomys sinensis troglodytes}, on a fine series of crania, mandibles, and parts of the body skeletons. This form had previously been described as a species on a much smaller sample by Matthew and Granger (1923). The large series of fossils, the completeness of the skulls and the proximity to Recent time in the age of their fauna permitted Colbert and Hootje to make a critical evaluation of the characters in their sample. Structural features that differentiate the living species of \textit{Rhizomys} were found to be constant in all three subspecies studied.

Comparison with the two living subspecies \textit{R. sinensis vestitus} and \textit{R. sinensis davidi} was made by simple statistical studies. It was found when the population samples of all three were studied that the Yenchingkou form, though comparable in size to \textit{vestitus}, differed constantly from both \textit{vestitus} and \textit{davidi} in certain minor characters. The skulls were relatively narrow, the teeth were relatively small, the ratio between the length of the molar teeth and the length of the skull was lower, and the ratio of mastoid breadth to the skull length was low. Other ratios were fairly constant in the three subspecies, “showing that the differences in the skull are at best but slight in these various Recent and fossil \textit{Rhizomys}.”

This comparison with characters in closely related living subspecies offers one of the best controls in an evaluation of fossil mammalian samples. The authors have demonstrated insofar as possible that the characters in the fossils are of approximately the same rank as those in the subspecies of the living bamboo rats. Thus both vertical and horizontal subspecies, as the terms are frequently used, are grouped together. The authors suggest that the fossil subspecies, \textit{trogodytes}, may be directly ancestral to one of the living subspecies, \textit{vestitus}, but they admit these may be separate lineages diverging from a common stem.

The subspecies proposed in other genera in the Yenchingkou by Colbert and Hootje are not as well represented as the sample of bamboo rats. Some of these could represent distinct species and not subspecies of the living species. This I think is quite possible in their examples of \textit{Crocuta} (spotted hyena) and \textit{Elaphodus} (tufted deer).

A comparison of some of the living species and subspecies of \textit{Peromyscus} (white-footed deer mice) in the total length of the molar series should give some idea of the difficulties to be encountered by the paleontologist in recognizing subspecies in the fossil record. The length of the tooth row in small rodents is one of the most useful characters frequently available in Cenozoic fossil samples that can be used in specific and subspecific determinations.

Measurements in millimeters were taken from specimens in the Museum of Vertebrate Zoology, University of California. The samples of species and their subspecies were selected at random in
the museum collections. The oldest and the youngest specimens were not measured. Five species were selected with the numbers in the samples ranging from 8 to 22. All four tooth rows in each individual were measured. The mean and its standard error, the standard deviation, and the standard range are indicated for each of the subspecies in Figure 11. The size of each sample is indicated by the numbers at the base of each column. Letters at the top of each column are abbreviations for the subspecies.

There is overlap in this character not only in the subspecies but also in the species. If these maxillary and mandibular tooth rows were to be encountered as fossils without the other controls available in living animals it would be impossible to recognize their affinities. Examples of this kind have led some paleontologists to the conclusion that most fossil species are of greater scope than the living species. In dealing with fossils, then, the judgment of the investigator must be relied upon in proposing the taxonomic rank of the samples before him.

It would seem that Pre-Pleistocene subspecies of the same magnitude of Recent subspecies will be extremely difficult if not impossible to establish. I do not infer that we should not attempt to recognize infraspecific categories in the fossil record nor am I convinced it is impossible to do so in all instances, even though we are hard pressed to find proof of their validity. I do believe nothing is gained by naming subspecies just because it is logical to assume they are represented in our samples.

It is absolutely unique and unrepeatable. This is because an individual of a sexual species has a genotype which is quite unlikely to occur in any other individual, or to recur in the future, or to have existed in the past. Suppose that a haploid chromosome set has only 1,000 genes, each gene capable of producing by mutation only 10 different allelic variants. Both estimates are certainly conservative; at least in higher organisms the number of genes is doubtless above 1,000, and most of these genes can produce more than 10 alleles. But even these over-conservative figures would mean that the potential number of gene combinations which might arise owing to the processes of gene segregation and recombination would be of the order of $10^{660}$. This is a completely fantastic figure, since it is very much greater than the estimated number of electrons and protons in the Universe.

This fantastic number has, however, a quite simple and concrete meaning. The number of genotypes which a living species is potentially capable of producing is immensely greater than the number of gene combinations which can ever be real-
ized. But, of course, the genotypes which exist are mostly those which possess some adaptedness to the environment. Sewall Wright has suggested a very useful metaphorical picture to visualize the situation. The existing genetic endowments of different organisms are concentrated in groups, which inhabit a finite number of “adaptive peaks.” This can be represented by a symbolic diagram which looks rather like a topographic map, wherein the elevation corresponds to the fitness of a genotype in some environment or for some way of life. Suppose, then, that Mount Hood is the adaptive peak occupied by some exceptionally well-adapted species, say by man. Mt. Jefferson, and Sisters, and some minor adaptive peaks are occupied by other species, say by monkeys or apes.

The peaks are, however, separated by low ridges or by valleys. In terms of the Wrightian metaphor, the valleys correspond to the gene combinations which are adaptively valueless, and which do not exist either because they have never been produced, or because they have been eliminated by natural selection. There are no genotypes intermediate between that of the human species and those of apes or monkeys. This metaphorical picture is equally suitable to describe the situation in any group of organisms—in sexually reproducing and in asexual ones, in mammals and birds as well as in microorganisms. Everywhere the existing genotypes are grouped into arrays, and these arrays “inhabit” adaptive peaks separated by adaptive valleys, the latter symbolizing the missing intermediate links between the existing groups of genotypes.

This simple fact, that the organic variation is not only great but also discontinuous, is exploited by the naturalists and the classifiers for the practical end of making a convenient and “scientific” system and a catalog of organisms. How does a systematist do it? He identifies the groups of related genotypes occupying the various adaptive peaks, hills, ranges, and mountain systems, and calls them species, races, genera, families, etc. Mt. Hood, Jefferson, and Sisters represent the adaptive peaks of, say, three species; the Cascade Range is a genus; the Sierra-Cascade system a family, etc. The passes are the gaps which separate the species, the Willamette Valley is a gap between genera or families, etc.

Now, it may seem quite arbitrary which adaptive hills or peaks or ranges you will call races, and which species or genera. In asexual organisms it is, indeed, arbitrary; any array of genotypes may be called a species, if this seems convenient. In sexually reproducing and cross-fertilizing organisms there exists a restriction which makes this arbitrariness much more limited. In asexual forms, individuals are independent, except by virtue of common descent; in a sexual species individuals are multiconnected by the bonds of marriage and family relationships. Genetically, the bond between individuals of a sexual population is the bond of gene exchange. Individuals of a sexual species, such as man, are members of the same breeding group. The species, man, is an interbreeding population, or rather a group of interbreeding populations. In a sexual population, the individuals draw their genes from a common source, the gene pool; and, unless they die childless, the genes of individuals return again to the gene pool of the population. The genetic endowments of the generations to come will be derived from this gene pool.

Sexual reproduction furnishes the biological bond which attests to the validity of one category of systematics—the species. From now on I shall be speaking only about the sexually reproducing organisms, leaving the rest in the care of Professor Stanier. Now, among sexually reproducing organisms there is a critical stage of the evolutionary divergence of forms of life. This is the stage when the gene pool of the ancestral species splits up into two or more derived gene pools of descendant species. The significance of this stage in the process of evolution is very great: this stage makes the evolutionary divergence irreversible. So long as unrestricted hybridization is possible, a group of Mendelian populations—call them races, subspecies, breeds, what you will—may get into the same melting pot, and their gene pools may fuse together into a single gene pool of a greatly variable population. Thus, races of the human species came, as a result of development of civilization, to exchange genes more and more frequently, and some of them have ceased to exist as separate entities.

The process of speciation consists in development of reproductive isolating mechanisms which make the gene exchange between populations difficult or impossible. Quite a number of different mechanisms may bring about reproductive isolation; it may be sexual or mechanical or temporal isolation, or inviability or sterility of hybrids, or a combination of some or all of these. The important thing is that when the process of speciation is completed, that is to say, when the reproductive isolating mechanisms have become finally estab-
lished, the evolutionary divergence is irreversible. Populations, races, subspecies are genetically open systems; they stand in communication with each other, or are capable of such communication. Species are genetically closed systems which pursue their separate evolutionary courses.

Professor Mayr has stated, quite correctly in my opinion, that the species concept described above is not some special genetic species concept. It is a general biological species concept. G. G. Simpson wrote that the taxonomic species is an inference of morphological species, and the morphological species is an inference of biological species. There is one important fact which should be clearly realized: the frequency of situations in nature in which it is a matter of opinion whether you are dealing with a single species or with two or more closely related species is really exceedingly small compared to the situations about which there is no difference of opinion at all. For example, the domestic cat and the lion are different species. No one can have any doubt about this. Not only is there not the slightest doubt as to whether an individual is a lion or a pussy cat, but we know that the gene pools of these species are thoroughly separate. Similarly, there is no question that the pussy cat and the Siamese cat are not different species but different races, or breeds—at any rate, members of the same species.

There is no doubt that man, chimpanzee, and gorilla are different species. There is also not the slightest doubt that human races are races, not species, even though a strange book was published a few years ago in which the author contended that there are five living human (or subhuman?) species. Well, in a democratic society we have to put up with publications of this kind from time to time.

In some cases biologists find it hard to decide whether a given group of populations should be considered as members of a single species or of two or more species. Such cases are much talked about by biologists, but not because of this frequent occurrence. Systematists, geneticists, ecologists, and biologists in general keenly search for such situations, because they are interesting and profitable as materials for research. We are glad when we find a difficult "borderline" case between race and species.

We can safely say, therefore, that in a vast majority of cases the "old-fashioned" species coincide with biological species. The ability of primitive people to identify species is evidence that species do have objective validity. I would like to add one of my observations to Professor Mayr's story of Papuan ornithologists. In equatorial Brazil I was privileged to watch the work of illiterate tree specialists, who identified the species of jungle trees (and gave them names which were half-Indian and half-Portuguese) more proficiently than did scientific botanists with their Latin names. However, there are a limited number of situations in which the biological species and the species of systematists really do not coincide, and such situations are worth analyzing in detail. Most interesting are the so-called sibling species, which are pairs or groups of related species, that are morphologically very similar or identical, and yet by any reasonable biological criterion have completed the process of speciation.

The sibling species Drosophila pseudoobscura and Drosophila persimilis were first distinguished in 1928 by Lancefield, who found that these species produced sterile male hybrids when intercrossed in the laboratory. Since then a great deal of work has been done with them, and I shall briefly review the evidence which shows that they are indeed separate species. Until recently they were considered completely indistinguishable in morphology. Some 20 years ago I asked an eminent authority on insect morphology to examine the genitalia of males, in the hope that a distinction may be found. This authority, who was incidentally convinced that insect species must be distinguishable by male genitalia, sent me a letter beginning with the words: "By God, they're completely alike." But the authority was wrong; for Dr. Rizki, who was then a graduate student in our University, found a very minor difference in the shape of the genital armature in males. More recently, Dr. Lewontin, Mr. Cooper, and Mr. Spasskai have discovered still other slight but significant differences in the male genital structures. The result is that we now can distinguish males of D. pseudoobscura from D. persimilis, although to do so a fairly high magnification is required, and macerated and cleared preparations of the genitalia are desirable. The females of the two species cannot, however, be separated by inspection.

The two species differ in geographic distribution. Drosophila pseudoobscura occurs from British Columbia to Guatemala, and from the Pacific to the Rocky Mountains and Texas. The distribution area of D. persimilis is included in that of D. pseudoobscura; D. persimilis occurs from British Columbia to California, and from the Pacific to just east of the Sierra Nevada-Cascades moun-
tain chain. There is, thus, an incomplete geographical isolation between the species.

Some ecological isolation is also present. In the region where both species occur, *D. pseudoobscura* generally prefers warmer and drier, and *D. persimilis* cooler and more humid habitats. For example, in the Sierra Nevadas of California, in the foothills, *D. pseudoobscura* is the predominant or the only species, while in the Alpine Zone *D. persimilis* is the near monopolist. At intermediate elevations the population of both species may be about equal in density.

The two species are partly isolated by sexual isolation. This can easily be shown in the laboratory if a mixture of virgin females of both species is placed in a container with males of one of them. By dissection of the sperm receptacles of the females and examining them for presence of sperm, it can be shown that matings within a species occur more frequently than matings between species. The degree of isolation varies depending upon the environment and upon the strains used. Some years ago, E. Mayz found with the strains he used that isolation was stronger at high than at low temperatures. Koopman found that the degree of isolation may be increased by selection; the mating preference is influenced by genetic modifiers in both species. Yet it would appear that sexual isolation in nature is much more intense than in laboratory experiments. During the six summer seasons that I have observed *Drosophila* at Mather, California, no hybrids at all were found during five summers, although the two species occur there with roughly equal frequencies. Finally in the summer of 1954, we collected one female of *D. persimilis* inseminated by *D. pseudoobscura* males, and a female of *D. pseudoobscura* inseminated by a *D. persimilis* male. The sexual isolation is, thus, quite strong but still not complete.

There is some behavioral difference between the species; i.e., copulating pairs of *D. pseudoobscura* are relatively more frequent in the afternoon, while those of *D. persimilis* are more frequent in the morning. The F₁ hybrid flies obtained in the laboratory are as vigorous as are the parental species; thus the species are not isolated by hybrid inviability. The hybrid males are, however, absolutely sterile. This sterility is due to profound disturbances in the process of spermatogenesis which cannot be described here. Hybrid females are fertile and deposit as many eggs as do females of the pure species. Backcross progeny can be obtained by crossing the hybrid females to males of either parental species; the individuals composing these progenies, however, are much less vigorous than either the F₁ hybrids or the parental species. This constitutional weakness of the backcross progeny is caused by the hybrid chromosome complement which is present in the mother's body and in the eggs themselves before meiosis. Just why the hybridity does not interfere with the somatic vigor of the hybrid females, but makes their eggs abnormal, is not clear. At any rate, the result is that gene transfers from one species to the other can be made in laboratory experiments, in which the backcross cultures are kept in optimal conditions of abundant food, favorable temperature, etc. Under more rigorous conditions, for example in the "population cages" used for laboratory experiments on *Drosophila* populations, the backcross hybrids are nearly or entirely wiped out.

Now we can evaluate the situation as it appears in the light of the data summarized above. Members of the two populations, which we call *Drosophila pseudoobscura* and *Drosophila persimilis*, are virtually indistinguishable morphologically. At any rate, a museum systematist examining specimens pinned, dried, and shrunken in the conventional way of entomological collections is unable to write the determination label naming the species of a specimen. All he can do is to say that the specimen belongs either to *pseudoobscura* or to *persimilis*. Now, systematists like order and clarity, and they are inclined to be disturbed by such hesitation.

Yet it can be shown conclusively that *D. pseudoobscura* and *D. persimilis* are genetically closed systems; they do not exchange genes; they are as "good" species as are, for example, the cat and the lion. Apart from the evidence of reproductive isolation summarized above, their status as good species is attested by the following additional evidence. Natural populations of both species are variable with respect to the gene arrangement in their chromosomes; each species has a certain number of variants, inversions, which the other species does not have. Now, if the two species would hybridize from time to time in their natural habitats, then we should discover the inversions characteristic for *D. pseudoobscura* at least as an exceptional feature in some individuals of *D. persimilis*, and vice versa. We have never found such exceptions. Therefore we must conclude either that the gene exchange between the two species never occurs, or if it does on rare occasions then the natural selection eliminates the foreign genes from the species populations. Either
way, the conclusion is unavoidable that we are dealing with two genetically closed systems of two biological species.

It will be asked by some traditionalists among the taxonomists, granted that D. pseudoobscura and D. persimilis are biologically distinct species, do we have to give them different specific names and thus make a difficulty for the museum taxonomist? This is a reasonable query. There are two problems facing us, the biological and the nomenclatorial ones. Biologically, these are different species. But whether they should or should not be given names, is a matter of convenience and of nothing else. If Drosophila were a group of insects studied exclusively by museum taxonomists, the problem would be solved automatically; the question of giving them names would not arise because the existence of these species would not be suspected. But Drosophila happens to be interesting not to taxonomists alone; it is studied also by geneticists, ecologists, and biologists in general. We have to talk and to write about these species, and to do so it is easier to refer to them by names than to get entangled in the verbal contortions of referring to them as races or varieties which are neither races nor varieties.

The same reasoning applies, I believe, to other instances of sibling species, of which a fair number are known at present. To cite an example, among the anopheline mosquitoes, the species are often not distinguishable as adults, but may be distinguishable as larvae or in egg masses. Thus, the old species Anopheles maculipennis proved to be a compound of at least six sibling species. Should one describe and name these species or should one refrain from doing so? The answer is easy. Anopheles is a group of insects which are far more important to epidemiologists and medical men than to museum taxonomists; some of the sibling species are vectors of malaria while others do not transmit malaria. A refusal to distinguish these species would hardly increase the practical utility of taxonomy as the basis of other biological sciences.

To summarize: The existence of sibling species has not made an unbridgeable gap between systematics and genetics. Quite the contrary is true. Sibling species are the exceptions which can indeed be said to prove the rule. The species of systematics are the biological species. But to demand that species be always distinguishable in pinned and dried specimens in museum drawers is like suggesting to a modern surgeon that he refrain from using any instruments and techniques which were not used by the surgeons of the 18th century.

**Dr. Mayr:**

I'm sure that this most illuminating discussion on the genetic aspects of species has raised a great many questions, and I hope that the audience doesn't hesitate to ask them. One point that occurred to me concerns the adaptive peaks. Special combinations of genes make populations, and therefore the populations of which species are composed, specially adapted. This raises a question as to the amount of genetic variability that a gene pool can incorporate. I would like you to clarify this point because one or two recent workers have gone so far as to say that there should be an evolutionary tendency or a selective advantage for a species to incorporate not an optimum, but an unlimited amount of genetic diversity in its gene pool. I feel there might possibly be some objection to that.

**Dr. Dobzhansky:**

This is, indeed, an unsettled and a challenging problem. I quite agree with Dr. Mayr that the amount of variability contained in a species is in itself an adaptive trait. When a species or a Mendelian population of any kind faces a diversified environment, it can conquer the environment by becoming genetically variable. A variable species will, other things being equal, contain more genotypes adapted to many different environments than will a genetically uniform species. The saying that it takes all kinds of people to make a world is applicable to man, and it takes all kinds of genotypes to make the worlds of many other species of organisms.

On the other hand, too much variability lowers the immediate fitness of the population in which this variability occurs. This is because many variants will not be useful in some environments, and still other variants, mutations that occur, may be useless in all environments. So, a balance is struck: a species contains enough variability to take care of the environmental diversity in space and in time, but too much variability is harmful and is eliminated by natural selection.

Why Drosophila, and some other genera of insects, are very rich in sibling species, while other insect species are strikingly different morphologically, can be answered only by a speculation, or, if you wish, by a tentative working hypothesis. It may be that in Drosophila flies the external morphology has been developed in the process of evolution to a state near perfection. By
“perfection” I mean simply that, in the environments in which these flies live, modifications of the external morphology are much more likely to be harmful than useful. But this has not stopped all evolution of the genus Drosophila. There is plenty of room for physiological variability which adjusts these flies to ecological diversity that they are facing in nature.

**QUESTION:**
You referred to genetic variability. Is this variability as pronounced for physiological characters or fitness as for morphological characters used by taxonomists?

**DR. DOBZHANSKY:**
I find this difficult to answer, and I don’t think it can be answered for all organisms. Now for Drosophila, in particular, I believe that such was the conclusion reached. The differences between, not only geographic races of the same species, but even between obviously different species, are very frequently physiological rather than morphological in nature. I quite agree with Dr. Mayr, to some extent at least, that our sense organs limit our methods of investigation. After all, if we had different means of investigation, we would perceive different qualities of the organisms which may change our opinion on their biological relationships. To return to the question, in some organisms, at least, variability is physiological more than morphological. Now please remember that any morphological difference is simply a reflection of an underlying physiological difference. There can be no morphological differences without the physiological, and it is possible to have a physiological difference without a morphological one. I’m not sure I answered the question, but that is as near as I can get.

**DR. MAYR:**
I have one or two more questions here but I think we’d better keep them for the later question period in order to be sure that we don’t get too far behind in the program. I would like to take this opportunity to thank Professor Dobzhansky for a particularly brilliant performance.

**General Discussion**

**DR. MAYR:**
I believe we now have time for a period of some more general discussion. First, a somewhat amusing question that I can answer very quickly.

**QUESTION:**
Is there any possibility that there are sibling species in modern man, so far not recognized?

**DR. MAYR:**
This is an intriguing possibility, but since sibling species are reproductively isolated populations and since there is no evidence that any human populations are reproductively isolated from any other human populations, I think we can say very definitely and decisively, that there are no sibling species in modern man.

**QUESTION:**
Another question takes us a little off the subject of this Colloquium; it asks: “How does one differentiate a subgenus from a genus?”

**DR. MAYR:**
To answer this question properly would lead us into the whole philosophy of the naming of the higher categories and also into the question of splitting versus lumping. Is it more convenient to have the subdivisions of the genus designated by species groups, as is customary in Drosophila where one speaks of the obscura group of species and the affinis group of species, or should one designate even rather slightly different species as subgenera? Although the use of the subgenus may be convenient in very large genera, my own personal inclination is to avoid the use of subgenera because of the load on the memory. Trying to remember the name of a subgenus is just as great a task as trying to remember the name of a genus, and we should avoid them if we can do without them. In spite of all refinements we can never reproduce in nomenclature the very intricate details of relationship and of degrees of difference. Nomenclature is but a very loose approximation to classification and classification to relationship, and we should not try to make it too complex.

**DR. HILLEMANN:**
Please speculate on the evolutionary origin of viruses of rickettsiae.

**DR. STANIER:**
I think, as I hinted in my talk, we have reason to believe that the bacterial viruses are evolutionary, in some way, an offspring of the bacteria themselves. In a sense the genetic systems of bacteria and bacterial viruses are fluid and capable of a sort of interpenetration through time. The type
GENERAL DISCUSSION

of work which has led recent investigators, particularly students of the lyogenic bacterial viruses, to these conclusions, has not been carried out on the plant and animal viruses. And I feel it's much more difficult to make any speculations about the nature and origin of those two viral groups. I wouldn't be surprised if it turns out that we've been talking about three groups of entities, which in origin, structure, and function are only superficially similar. Eventually we may have to postulate quite other origins for plant and animal viruses, plant viruses in particular. As for the rickettsias, I feel that we simply don't have enough biological knowledge at the present time to make any reasonable speculation. We don't know nearly enough about their biological behavior. No one has started an investigation of these entities. There's a sort of single-minded concentration that has been diverted in the last 15 years to the viruses.

Dr. Mayr:

I would like to say one word more about sibling species because in one or two of the questions I thought I noticed a slight misunderstanding. Sibling species, so far as I can tell, are in no way different from other species except that to the human eye, to the eye of the taxonomist, they are less distinct. In all the cases where sibling species were studied genetically, they seemed to show roughly the same amount of genetic difference as other species that were more distinct morphologically. Furthermore, degree of morphological difference is only one of many possible measures of relationship.

Anyone who watches the courtship of two sibling species of Drosophila placed together in a glass vial will observe that they can distinguish each other quite well. It has been shown that olfactory clues are exceedingly important in this species discrimination. Now if we had an olfactory sense organ, as sensitive as that of Drosophila, then some of these sibling species of Drosophila would "look" strikingly different from each other. In other words, if we could add olfactory character to the morphological characters, such sibling species at once would no longer be sibling species.

Dr. Boyd:

To what taxonomic category would you assign, first, the major phenotypic variants of modern man, as for instance the caucasoid, mongoloid, etc. and, second, the less obvious variants such as nordic, alpine, mediterranean, etc.?
era and species, and many changes in the meaning of the categories are unavoidable. Hence, the agreement on the basic principles is quite close, but people working with very different materials face very different problems and in the application of the general principles they very often come to, at least technically, very different conclusions.

**Question:**
What is the current opinion regarding “physiological” species? How are they treated taxonomically?

**Dr. Mayr:**
First, all species are physiological species, so to rephrase the question: What is the taxonomic status of species which one cannot differentiate by morphological characters, only by physiological ones? Such species are nowadays included among the sibling species, and whatever we said about sibling species also applies to them. If they are important for either genetic or other practical reasons, as Professor Dobzhansky explained, they will be treated taxonomically as full species. In other cases they very often are not formally described as species, as for example the physiological species in Paramecium are simply described as “varieties,” although those who work with Paramecium are fully aware of the fact that, biologically speaking, they deal with full species. There are a few similar cases where, for practical reasons, the workers in the field have decided not to name sibling species formally.

Here is a question which may or may not be flattering to us systematists.

**Question:**
Is not systematics an art rather than a science?

**Dr. Mayr:**
This question permits me to emphasize the art part and consider myself an artist, or to emphasize the science part and to consider myself a scientist. I would like to say, in order to get the best of the argument, that systematics is both an art and a science. Professor Stirton pointed out that some workers, even with scanty evidence, usually make the right choice and describe things as species and genera which additional material shows clearly to be good species and good genera, while other workers who are less “artistic” publish many synonyms. Thus the application of principles and in the recognition of taxonomic characters there is as much art in systematics as for instance in the work of a skillful diagnostician or physician who can make the right diagnosis of a disease with just a few symptoms. The good taxonomist, likewise, has enough experience so that from comparatively few clues he can arrive at the right decision and say, “This specimen is nothing but an aberrant individual of a known species,” or “This specimen, or this piece of this specimen, is a new species or a new genus.” He may propose a classification which a great deal of additional material and analysis subsequently shows to be completely correct even though it was based on very limited information.

**Question:**
Since there are adjustments to the biotic environment and also adjustments to the physical factors in an environment, these latter particularly pronounced in the temperate and arctic zones, which type of evolution is more likely to produce the major new forms of the future and why?

**Dr. Mayr:**
Now there’s something close to one pronouncing one’s fate. I must say that I belong to the evolutionary school or church, whichever you prefer, that believes in the tropics. Having been to the tropics I can attest to the enormous diversity of nature, and of life, and the incredible number of interesting specialized adaptations. There we have so many attempts at finding new adaptive peaks, that some are much more likely to lead to new evolutionary advances and eventually to new higher categories than the adjustment to the rigorous climate of the temperate and arctic zones. Quite obviously, I cannot prove this, nor can anybody find good evidence to contradict me.
SUMMATION
Systematics and Modes of Speciation

ERNST MAYR

I think we have summarized the scope of the proceedings two or three times, so rather than go into too much detail I shall merely try to bring out a few points that seem to be of particular importance. One is, and this is particularly true for the genetic mechanisms, that there is no basic difference between plants and animals. In both zoology and botany there is an increasing tendency for a biological definition of the species. Such a biological definition of the species is possible only in sexually reproducing organisms where the joint gene pool of the populations, of which the species is composed, forms the unifying element. One other result is that the gap which exists between species is not only a reproductive one, supported by isolating mechanisms, as well as a genetic one, but in the vast majority of cases also a morphological one as pointed out by Professors Lewis and Dobzhansky. As a taxonomist I must say that it is certainly fortunate that there is such a coincidence between the reproductive and morphological gap. Gene exchange between coexisting species is something that occurs frequently in plants but is very rare in the higher animals. Although morphological differences normally exist between species, we occasionally have perfectly good species by every single criterion but not clearly distinguishable by clear-cut morphological differences. Professor Dobzhansky gave a very beautiful analysis of such a case in the two sibling species of Drosophila, D. pseudoobscura and D. persimilis.

What is doubtful is the application of this species concept of the higher animals and plants to microorganisms. Let me repeat once more the type of species definition that is nowadays usually favored: Species are groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups. In microorganisms, however, there is often a complete absence of sex and only a limited amount of gene exchange between individuals, and in these cases the usual species definition faces difficulties in application. Perhaps of more consequence, at least in the bacteria, is the fact that the evidence rather strongly favors an essentially haploid condition during the major part of the life cycle. In such haploid organisms every gene is exposed to the full rigors of selection, and even occasional gene transfer must be able to weather this rather strenuous condition. Nevertheless, the presence of bundles of related lines or clones seems to suggest cohesive forces which have not yet been fully explained. The difficulties in paleontology are of a different nature. It is evident that the breeding system and the system of species and infraspecific categories of the extinct species, when they were still in existence, was the same as in living ones. The difficulty with fossils is that our evidence, by necessity, is limited. Much of the information needed in order to classify samples found in nature is not available, and the species of the paleontologists, as Simpson has said, are an inference derived from the morphological nature of samples on the probable genetic nature of the material.

There is fairly complete agreement among the participants of the Colloquium that in the higher plants and animals only one of the infraspecific categories, the subspecies, is meaningful for the taxonomist, and only one other for geneticists and biologists, the population. The application of the biological concepts of species and populations to the material of the taxonomist is often difficult. This is true not only for material like fossils, where the evidence is very incomplete, but even in living species because the populations of which these species are composed continue to evolve. We are often confronted with situations like circular overlap where the same material permits two opposing conclusions.

I said this morning that I would defer a discussion of biological systematics until tonight. It has undoubtedly become clear to every member of the audience by now that systematics is no longer a "dry-as-dust pigeonholing of specimens," as taxonomy used to be described. To an increasing degree systematics has become a branch of biology, the science of life, and the biological aspects of systematics are getting more prominent every day. This new spirit of taxonomy has not passed unnoticed in biology departments, and the cooperation between the museum taxonomist and experimental biologist, which for a long time hardly existed, has been reestablished and is getting
closer all the time. For this new spirit in taxonomy Julian Huxley has coined the term, “the new systematics.” There are many ways by which one could describe the new systematics, but the simplest way is to say that the new systematics is characterized by its emphasis on the study of populations and on the study of the biological significance of species. As a student of populations and as a student of species, the systematist is making major contributions to the general theory of biology.

I am sometimes asked: “Where in biology does systematics really fit in?” An attempt to answer this question leads us on a little excursion. If we go back through the history of biological science, we find that originally the science was split into zoology and botany, a split which to some extent still exists. These main branches were later subdivided into fields like embryology, genetics, physiology, anatomy, etc. Recently biologists began to feel that these compartments were not quite natural, and Paul Weiss for one proposed still another classification, containing such subdivisions as cellular biology, regulatory biology, genetic biology, environmental biology, etc. I have been thinking about these classifications for quite some time and have come to the conclusion that all miss the point in some way. Basically there are only two kinds of biology, functional biology and evolutionary biology. Functional biology is that branch of biology where it is asked: “How does something function? How does something operate?” In this branch of biology the method is that of the experiment, and the material is a single zygote, a single individual, or part of one. The other branch of biology, about which we heard a great deal today, is evolutionary biology. The questions asked in this field concern the meaning of things, the significance, the evolution, the change. The method is basically that of observation and of comparison, whenever possible corroborated by experiment. The material does not consist of a single organism or a single cell, but of the comparison of many different units and of the study of populations. This distinction between functional and essentially evolutionary aspects goes through many branches of biology. In genetics, for example, there are population geneticists and physiological geneticists. The population geneticists ask the questions of evolutionary biology. They study populations; they inquire into the significance and meaning of things; they study changes in frequencies of genes, inquire into fitness and viability under different circumstances.

The physiological geneticists study the physiology of the genes, the nature of gene products, the enzymes, and investigate how these substances affect growth and differentiation. The gene physiologist feels close to the experimental embryologist, to the biochemist, or to the cellular physiologist, while the population geneticist has interests similar to others working in evolutionary biology, namely, the paleontologist, the botanist, and the ecologist. It should be quite clear now where systematics belongs. Systematics is one of the important branches of evolutionary biology; it is in some respects both the basis of this field and the final goal of this field because it ultimately incorporates all of its conclusions.

There is another way of looking at the field of systematics from a more general viewpoint, and that is to inquire as to what unit of life it studies. No doubt many of you are familiar with the concept of levels of integration. At the lowest level are the nuclear particles, electrons, protons, neutrons, etc., which are integrated into the next higher level, that of the atom. These in turn are integrated into molecules, and as you go up the line you come to the large integrations of the organic nature, the components of the cell, and finally the cells. Distinct branches of biology are devoted to the study of cell life: cytology, cyto-genetics, and cellular physiology. Cells are combined into tissues studied in histology, and tissues into organs studied by anatomy and physiology. The next higher level consists of individuals, studied in psychology and sociology, while populations and species are a still higher level. Populations and species are exceedingly important levels of integration, levels that up to now have been rather neglected in most biology departments.

There are some rather specific reasons why species are so important in the field of biology. They are important because they are a crucial unit in evolution, in ecology, in the behavior sciences, and in applied biology. I am afraid I cannot cover all this tonight, but I will attempt to discuss some of these points. A perfectly legitimate question which most biologists probably do not ask themselves is, “Why are there species?” Professor Dobzhansky has already given a very good answer to this question, and I am merely paraphrasing his comments. One way of realizing why there are species is to imagine a universe in which there are no species, but only individuals, and each individual is of a different genetic composition. Let us assume that any individual can potentially mate and reproduce with any other one. Every individual
would then be the core, the middle point, in a universe of concentric circles of more and more different individuals. It is very obvious that if a superior gene combination would be produced by the accident of genetic recombination, that highly adaptive superior combination would be broken down again by reproduction in the next generation and would be lost. This is, as Professor Dobzhansky explained, the real reason for species. In a species-less universe, the chance of finding a genetically similar mate would be very small. Species are protective devices for superior, coadapted gene complexes which thus have a much reduced possibility of outbreeding with other individuals. They can outbreed only with genetically similar members of their own species, and not with individuals that are as different as one would find in a species-less universe. Each species produces local populations everywhere which are adapted for local conditions, some of which manage to enter a new niche. And whenever, in the course of the evolution of the earth, new niches turn up, they are very quickly filled. In turn, each evolutionary event, each development of a new species or of a new type of organism immediately establishes a new vacant ecological niche which sets up an evolutionary premium for being filled. Here, then, is another reason for the origin of species.

It would be too time consuming to discuss the question of the origin of the species in detail; so I will attempt to summarize it in a few words. Basically there are three theories as to the origin of species. Let me emphasize that “the origin of species,” and this is one point which Darwin more or less missed, means not merely evolutionary change, but the multiplication of species—that is, the division of a single gene pool into two separated, reproductively isolated gene pools. Naive attempts were made to solve this by suggesting that sometimes in a species an individual turned up which belonged to a new species. In other words, the attempt was made to explain speciation in terms of individuals and in terms of sudden jumps. This does not explain how one gene pool becomes divided into two. Except for the cases of polyploidy and the cases of some asexually reproducing organisms, we know that such instantaneous speciation does not happen. The second type of theory starts from the completely correct observation of ecological differences between sympatric species. It concludes from this observation that ecological specialization is the primary event in speciation and can take place without geographical isolation. Hence, this theory has been designated as the theory of sympatric speciation. It postulates that some individuals of a population invade a new ecological niche, breed only with each other (and not with other sympatric individuals of the parent species), and become in due time so different genetically that they can be considered a different species. As elegant and convincing as this theory seems at first sight, it raises many difficulties of a genetic and ecological nature when it is investigated more closely. As there are no well-established incipient cases, we must conclude that sympatric speciation is very improbable. This leaves only the third theory, that of geographic speciation. The theory postulates that new species originate if part of a species population becomes separated by extrinsic barriers and during this extrinsic separation develops sufficient genetic differences to serve as the basis of isolating mechanisms. When this population eventually comes back to the range of the parental species, it will be reproductively isolated; in other words, it will be a new species! Except for the case of polyploidy, this, as experimental data indicate, is the normal mode of speciation.

Another point is the importance of species in evolution. Huxley, in 1942, stated that species were without significance for long-term evolution. I disagree quite emphatically with that viewpoint. Every species is an integrated gene complex and an adaptive one; every species is an experiment in adaptation and in evolution; every species differs from every other species in its ecology and physiology. Thus, every species has a chance to make a minor or major evolutionary invention. Such a highly successful group as the insects, for instance, descended from a single ancestral species; so did the true mammals, so did the higher plants. It seems to me that the only way in which evolution has a chance to hit one of these highly improbable adaptive peaks is to send out an enormous number of exploring parties. Each species is such an exploring party, and each of these hundreds of thousands of exploring parties has a slight chance to find one of these highly desirable, new major adaptive peaks and start a successful new evolutionary line. I feel that in this respect species are very much like mutations, in that they occur constantly, most mutations not improving the genotype. Yet an occasional mutation fits into a genotype so well that it does lead to an improvement. Speciation, to my mind, plays much the same role on the major evolutionary plane as mutation on the micro-evolutionary plane.

Species play a major role in evolution, but
they are also important to other aspects of biology, particularly ecology. When two individuals meet in nature they meet as typical representatives of the respective species to which they belong. For example, the relationship of an individual red-tail hawk and a meadow mouse, or of a mountain lion and a deer, is that of a representative of one species with the representative of another. This fact gives the ecologist an opportunity to generalize and make predictions. One of the major subdivisions of ecology is that which deals with animal and plant communities, and it appears to me that much in this particular branch of ecology is purely descriptive (that the community as a whole may serve only as an aggregate of the species of which it is composed). There is really only one way to understand this ecological community and that is by studying the species of which it is composed. A greater emphasis on the component species will lead to a better understanding of the dynamics of community than we have at the present time.

There is still another branch of biology in which the species is very important, the branch which deals with the biology of the species itself. We have talked a good deal today about isolating mechanisms between species. They are phenomena of utmost importance in organic life, and although known for a long time, study had been limited to only a few of the isolating mechanisms, namely the sterility barriers common among plants. Sterility, however, is only one of many isolating mechanisms. You may remember the question that was asked today in one of the discussion periods, "Why do certain species keep separate in spite of the fact that they are perfectly fertile?" The reason is, as I explained before, that there are isolating mechanisms. What are these isolating mechanisms? In animals, the most important ones are behavior patterns, which is the reason why in the field the female Mallard does not "like" the male Pintail or vice versa. Professor Dobzhansky mentioned the two species, D. pseudoobscura and D. persimilis, which hybridize with a low frequency in the laboratory, but in nature hybridize so rarely that in six years of field work he found only two females that had been inseminated by males of the opposite species. The branch of biology dealing with the behavioral patterns which keep species separated includes much of what Darwin called "Sexual Selection." It explains a great deal about the song, the courtship dances of birds, the chirping of crickets, and other kinds of behavior. This very important branch of biology is entirely tied up with the species and has meaning only as a factor that provides and reinforces a barrier between species. It keeps the gene pools intact so that they do not become polluted by alien genes.

There is so much more one could say about the biology of species that one could just go on and on, but I do not want my enthusiasm to carry me away. Biological systematics has been the theme of this symposium, and I hope that it has become clear to the participants that systematics is a biological science which studies populations and species as living systems, that it deals with areas in the field of biology which are not properly taken care of by other branches of biology, and that systematics, with its ramifications, has established so many contacts with bordering fields, that it is particularly suited to help bring about and reestablish the unity of biology. I feel that even the students in the experimental and functional branches of biology, including the biochemists and physiologists, must realize that the species is a major phenomenon in nature, of greatest importance not only to the systematicist but to all other biologists. Until this point is clearly understood by every biologist, we will have only biological sciences but not a science of biology.

Dr. Stephen:

Thank you, Dr. Mayr, for your most lucid summary of biological systematics. The meeting is now open for discussion.

Dr. Boyd:

What in your opinion is the role of the holotype in the new systematics?

Dr. Mayr:

This is a technical question but one which is important in the field of systematics. The holotype is the specimen on which original description of a new species was based.

Dr. Boyd:

Does it always remain the objective standard of reference on which to base comparison to other organisms?

Dr. Mayr:

The answer must remain somewhat ambiguous. The question was asked by a geologist, and when one deals with paleontological material one cannot entirely escape the implications of this question. In other materials, it is now understood that the type has nothing whatsoever to do with the "typical" characteristics of the species. The type is clearly a nomenclatorial instrument. For instance, you may someday discover that a species
that you have been dealing with actually consists of two or more sibling species, and you will want to know to which of the species to restrict the name that was originally given to the whole aggregate. An examination of the type will tell you to which of the several species the original name belongs. When you prepare the description of a new species, you pay little or no attention to the type specimen because the probability that it would be exactly in the middle of the variation curve of every character of the species is so astronomically improbable that it will never happen. When you prepare your description you treat the type like any other specimen in your entire series. The significance of the holotype is purely nomenclatorial. I admit that in paleontology it is often uncertain which specimens belong to the same population, and the type is a little more important than in neontology. Yet, as far as the underlying philosophy is concerned, the type is merely the name bearer. G. G. Simpson very properly suggested giving up the misleading term type and to call this particular specimen the onomatophone, the name bearer, to designate its true function.

**Question:** Why is sympatric speciation improbable in cases in which reproductive isolation is seasonal or ecological as, for example, in overlapping groups of 17-year locusts or in physiological races feeding on different host plants?

**Dr. Mayr:**

Let us begin with the case of the 17-year locust. How do the different races of 17-year locust originate? The first problem. So far I have not yet encountered a single feasible explanation that does not postulate an original geographic isolation of these populations followed by subsequent overlap. At least in this case there is no conflict between geographic isolation and speciation, and even if these races became species it would not be a case of sympatric speciation. The other case concerns physiological races feeding on different host plants. I am quite familiar with the literature on this problem. I have gone back over the writings of Craighead and Hopkins and many other students in this field, and all I can say is that it does not contain a single case convincingly demonstrating sympatric speciation. Few host races are completely restricted to a single food plant, and those that are can never change to a new host. On the other hand, if a species of insects can get over to other food plants, why should it not be able to come back, and why can't other individuals from the original food plant get over to them, too? I admit that speciation by way of host races is a theoretical possibility, and I am very much interested in it. I would like to see a case of sympatric speciation established, and if it were done I suspect that it would probably be in the field of physiological races. However, all the evidence we have at present indicates that a complete switch-over to a new food plant will happen only in a peripherally isolated population where ecological conditions are sufficiently different so that there is a selective premium on having a different food plant. Only after the new form has become thoroughly established there, and has changed genetically, can it come back to the original range and occur side by side with the parental species. No final answer is possible because there are only a few dubious cases, yet the ones that have been proposed do far certainly do not seem to substantiate sympatric speciation through the development of physiological races.

**Dr. Selander:**

What is your opinion of phylogenetic study pursued in the absence of fossil evidence?

**Dr. Mayr:**

I would first like to ask the question: "Why would you call such a study a phylogenetic one?". In the absence of fossils all you can do is to speculate as to what the ancestor of something or other would have looked like judging from the present diversity of the forms. Every taxonomist, of course, repeatedly does this, and some fool themselves into believing that they are studying phylogeny. Paleontologists have burned their fingers a good many times by reconstructing the presumable ancestor of a group of forms on the basis of unspecialized characteristics or later fossils, only to find that they were entirely and absurdly wrong when fossils of the real ancestor were found. One of the loveliest examples of this is Man. What was the appearance of the common ancestor of such living forms as chimpanzee and modern man? If you go to writings of Haeckel, you find that he reconstructed a picture of the common ancestor of the two which is an exact intermediate. Actually, such a creature could not have lived at all. It would have been an impossible creature. When *Australopithecus*, who is certainly very close to the human line, was found in South Africa some anthropologists said at the time that it could not possibly be the ancestor of modern man because it was not evenly more primitive in all characters. On the contrary, in its tooth structure, the shape
of the tooth row, and the pelvis, it was already approaching modern man, while in its brain, its face, and its strong bones it was still like an anthropoid. For a believer in archetypes, such a creature with a mixture of characters of modern man and anthropoid could not have existed. Yet, it did exist and is probably very close to the ancestry of man. This again shows how dangerous it is to apply the name phylogeny to such mere mental constructs. I have suggested the term "dendrogram" for such a construction. This is a tree diagram for what many books have erroneously called a phylogenetic tree based on no fossil evidence whatsoever.

**Dr. Edmunds:**

What is the significance of the phylogeny in systematics?

**Dr. Mayr:**

Even before we had an understanding of evolution we had so-called natural systems. Linnaeus' principal work was called *Systema Naturae*, and many other authors spoke of "natural systems." With this term they designated a system based on the greatest similarity in the greatest possible number of taxonomic characters. When the theory of evolution became generally accepted a quick switch in interpretation was made and the taxonomic categories were explained as descendants from a common ancestor. On the whole, we try to establish in our taxonomic work such categories as we believe have descended from a single common ancestor. We believe that by this method we can guarantee that if we were to look at taxonomic characters that have not yet been studied they would support this system. We believe that such a philosophy and such a method would permit the greatest number of accurate predictions concerning characters that have not yet been studied. I am not going to list in detail all of the objections to this philosophy. I do know that outstanding taxonomists have stated that the real purpose of classification is a purely practical one. Most taxonomists waver back and forth between endorsing a purely practical approach and believing that the function of the biological classification is to try to have categories that are descendants from a common ancestor.

**Question:**

How would you criticize Goldschmidt's theory of evolution by a macro-mutation as opposed to accumulative micro-mutations?

**Dr. Mayr:**

I think I can criticize that best with the help of a metaphor. You are all familiar with the beautiful mosaics which were found in Roman and Byzantine buildings, consisting of hundreds, thousands, and tens of thousands of colored marbles. Goldschmidt, in a theory of systematic mutations, would make us believe that if we should take all these marbles off the wall, put them on a giant shovel, and toss them out on a plain surface another beautiful picture will result. This would not be the same as the original one but still another well-balanced and beautiful picture. I submit that the possibility of such an event is certainly exceedingly small. In other words, if Goldschmidt were right, one should find the world virtually populated with "hopeful monsters." This is not the case. While the believers in geographic speciation can demonstrate abundant cases of geographic isolates qualifying as incipient new species, I have yet to be shown a single probable case of an incipient species through a "hopeful monster."

**Question:**

Would you consider the opportunities for evolution among host-specific parasites?

**Dr. Mayr:**

In order to understand speciation in host-specific parasites it must be remembered that even host-specific parasites may be found on a different host at different localities. An occurrence in, or on, a different host is restricting gene flow just as much as is isolation on an island. Though the term geographic speciation may seem a little far fetched, speciation on different hosts is exactly the same phenomenon, being an interruption of the gene flow by extrinsic barriers. Whether it is called spatial isolation, or anything you please, speciation in host-specific parasites is, biologically and genetically, the same sort of phenomenon as is geographic speciation.

**Dr. Margach:**

If the major purpose of species is to protect advantageous genotypes, what role to this end would you assign to sibling species?

**Dr. Mayr:**

The answer was given by Professor Dobzhansky who pointed out that even where there are no morphological differences between species there
are numerous physiological differences. Indeed, there are presumably many more physiological differences between species than there are morphological ones, and it is evidently these physiological differences between sibling species which permitted and favored their speciation.

**DR. DE LAUBENFELS:**

Is not your third species concept always either morphological or genetic or simultaneously both?

**DR. MAYR:**

This is a matter of emphasis. In the third species concept one emphasizes the fact that a collective group of populations is exchanging genes or is able to exchange genes with each other. The fact that these populations are not identical morphologically, although perhaps not as different as are full species, is not part of the concept, and I believe it would only be confusing to add any other criteria. Of course, this third species concept is primarily a genetic one because it emphasizes the genetic unity that exists among all the populations that exchange genes with each other.

**DR. ANTHONY:**

If it is generally true that entirely new lines arise only from primitive stocks, is speciation from subspecies a progressively narrowing process to a highly specialized and impoverished gene pool?

**DR. MAYR:**

This question contains two misconceptions. One is that new lines originate only from primitive stocks. This has been a widespread idea, but it is not necessarily correct. If you look at the reptilian stocks that existed in the Mesozoic, you certainly would not have picked the highly specialized pseudosuchians to give rise to such a successful line as the birds. Or if you look at the lower vertebrates, there are hardly any more specialized forms than the coelacanths which gave rise to the land living vertebrates, unquestionably one of the most successful kind of animals that has ever existed. The idea that a stock has to be primitive in order to produce successful descendants is certainly not true. The second misconception is that evolution leads to a gradual depletion of the genetic reserve. Genetic variability is not only eroded away by selection, but it is also continuously replenished by mutation. At the same time, there are various mechanisms which prevent an all too rapid depletion of the gene contents, such as superior viability of heterozygotes, the complete recessiveness of genes, the changing environments that shift selection pressures and so forth. There is no evidence that higher organisms have fewer genes available for evolution than lower organisms; in fact, most likely the opposite is the case. There is no evidence for a steady trend toward a depletion of the gene reservoir during evolution.
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