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Editor

ROY WALDO MINER

VIRUS AND RICKETTSIAL CLASSIFICATION
AND NOMENCLATURE

BY

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ROY WILSON MINER

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CONTENTS

	PAGE
Virus Classification and Nomenclature. <i>By</i> SIR MACFARLANE BURNET	383
Concepts of Classification and Nomenclature in Higher Organisms and Micro-organisms. <i>By</i> ERNST MAYR	391
Viruses that Reproduce in Plants and Insects. <i>By</i> L. M. BLACK	398
Problems of Viral Nomenclature and Classification. <i>By</i> FRANCIS O. HOLMES	414
The Nature of Viruses in Relation to Nomenclature. <i>By</i> JAMES JOHNSON	422
The Rio Congress Decisions with Regard to Study of Selected Groups of Viruses. <i>By</i> C. H. ANDREWES	428
Advantages of the Linnean Binomial System for Plant Viruses. <i>By</i> P. LIMASSET	433
Possibilities of Generic Classification in Rickettsiae and Viruses. <i>By</i> GEOFFREY W. RAKE	439
Criteria for a Biological Classification of Bacterial Viruses. <i>By</i> MARK H. ADAMS	442
Discussion of the Problem of Imperfectly Known Viruses. <i>By</i> A. A. BITANCOURT	448
Virus and Rickettsial Classification and Nomenclature. <i>By</i> HERALD R. COX	455
Classification of Rickettsiae Pathogenic to Vertebrates. <i>By</i> J. D. W. A. COLES	457
Nomenclature of the Rickettsiaceae Pathogenic to Vertebrates. <i>By</i> CORNELIUS B. PHILIP	484
On the Nomenclature and Classification of Insect Viruses. <i>By</i> G. H. BERGOLD	495
Taxonomy of Insect Viruses. <i>By</i> EDWARD A. STEINHAUS	517
Criticism of Binomial Nomenclature as Applied to Plant Viruses. <i>By</i> F. C. BAWDEN	538
Psittacosis Group. <i>By</i> K. F. MEYER	545
The Lymphogranuloma—Psittacosis Group. <i>By</i> GEOFFREY W. RAKE	557
The Nomenclature and Classification of the Pox Group of Viruses. <i>By</i> G. JOHN BUDDINGH	561
Influenza Virus Group. <i>By</i> SIR MACFARLANE BURNET	567
Possible Classification of the Arthropod-Borne Encephalitis Viruses. <i>By</i> W. McD. HAMMON	568
On the Nomenclature and Classification of Arthropod-Borne Encephalitides. <i>By</i> PIERRE LÉPINE	574
Relationships Between Arthropod-Borne Viruses Based on Antigenic Analysis, Growth Requirements, and Selective Biochemical Inactivation. <i>By</i> ALBERT B. SABIN	580

* This series of Papers is the result of a Conference on *Virus and Rickettsial Classification and Nomenclature*, held by the Section of Biology of the New York Academy of Sciences, January 11 and 12, 1952.

The Coxsackie Virus Group. <i>By</i> GILBERT DALLDORF	583
The Coxsackie Group of Viruses. <i>By</i> JOSEPH L. MELNICK	587
Classification and Nomenclature of the Poliomyelitis Group of Viruses. <i>By</i> ANDREW J. RHODES	596
Discussion of Classification and Nomenclature of the Poliomyelitis Virus Group. <i>By</i> HILARY KOPROWSKI	601
Viruses of the Encephalomyocarditis Group. <i>By</i> JOEL WARREN	609
The Viral and Rickettsial Registry, U. S. A. <i>By</i> JOSEPH E. SMADEL	612
Plant-Virus Type Culture Collections. <i>By</i> H. H. MCKINNEY	615
General Discussion of Virus Nomenclature. <i>By</i> SIR MACFARLANE BURNET	621

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CONTENTS

	PAGE
Virus Classification and Nomenclature. <i>By</i> SIR MACFARLANE BURNET	383
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Viruses that Reproduce in Plants and Insects. <i>By</i> L. M. BLACK	398
Problems of Viral Nomenclature and Classification. <i>By</i> FRANCIS O. HOLMES	414
The Nature of Viruses in Relation to Nomenclature. <i>By</i> JAMES JOHNSON	422
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Classification of Rickettsiae Pathogenic to Vertebrates. <i>By</i> J. D. W. A. COLES	457
Nomenclature of the Rickettsiaceae Pathogenic to Vertebrates. <i>By</i> CORNELIUS B. PHILIP	484
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VIRUS CLASSIFICATION AND NOMENCLATURE

By Sir MacFarlane Burnet

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Probably, there is no difference of opinion amongst virologists that, were adequate knowledge of the interrelationships of viruses available, an accepted and workable nomenclature would be a desirable convenience. The same arguments that have been used in regard to bacterial nomenclature are also applicable to the virus problem. A worker actively studying a particular group of viruses is usually quite happy to go on using the names that, in one way or another, become attached to his virus strains. He may feel quite at home with "Columbia-SK," "MM," "Mengo," and "encephalomyocarditis" viruses, and realize that they are all closely related forms. For workers in other virus fields, for post-graduate students, or public health officers, for anyone, in short, who wishes to know the significance of virus investigations without making a whole-time study of virology, the position would be much easier if a name as expressive as *Mycobacterium* or *Clostridium* were available to cover that particular group of viruses and provoke an immediate mental picture of a certain complex of practically demonstrable qualities. An accepted nomenclature is still more desirable when the same virus is discussed in several different languages. I need not labor this point, nor does it seem necessary to look beyond the Linnean binomial system for the form of the names that might eventually be suggested. The general acceptance of a binomial nomenclature for bacteria and other asexual forms virtually eliminates any other possible system for viruses.

If, however, we would agree in principle that each "good" species of virus should have a suitable binomial and that we class related species in a single genus, we immediately come up against the requirement, which is the basis of modern systematics, that the nomenclature should be based on a classification with a natural, *i.e.*, evolutionary, significance. The crux of the matter is to decide what is the natural criterion for deciding which of all the clones of virus that have been studied are sufficiently alike to justify saying that they are all examples of one species.

Sometimes this is easy. I do not think there would be any controversy as to whether or not mumps and herpes simplex viruses represent good species. Each is responsible for a characteristic human disease that has been known, in essentially its present form, for centuries. When any strain of either virus is compared with others from different parts of the world, the differences among them are trivial compared with their common differences from any other known type of virus.

The modern developments in population genetics which, in the hands of Sewall Wright, Dobzhansky, and Mayr, have led to a much clearer understanding of speciation in higher organisms, are not directly applicable to agamic forms. Work on recombination of viruses will have to go very much further before we can even consider that the concept of access to a common gene pool

can ever be added to the current picture of virus reproduction as wholly clonal in character.

Nevertheless, even with due regard to the highly mutable character of viruses, the essential parasitism of viruses provides a very effective method of functional isolation and stabilization of the genotype. Perhaps an approach is possible if we compare the situation, not so much with the differentiation of higher organisms into *species*, but their higher level differentiation into genera, families, *etc.* Systematists agree that the species is a more precise natural unit than the genus or any higher category, yet to an outsider there still seems to be a considerable subjective element in the decision as to what is a species and what is a subspecies in certain groups. Similarly, one cannot escape the impression that the higher categories do correspond, to a large extent, to natural situations and are not wholly creations for the convenience of systematists.

In the most general terms, we might follow Sewall Wright's conception of adaptive peaks in the field of possible gene combinations into the situation with parasitic microorganisms. The virus of herpes simplex is the phenotype of a certain combination of genetic units which makes it uniquely fitted to survive in a given environment (which, in this case, is not only the human species, but also special anatomical, physiological, and behavioral aspects of that species). It occupies an adaptive peak, a peak which, from the uniformity of natural strains of the virus, is a sharply pointed one. There is, however, another environment in which the virus can survive indefinitely, under conditions not much more specialized than the natural ones. This is a "well-adapted experimental strain" on the chorioallantois of the chick embryo. Here, there is not only the new tissue, but also the requirements of the experimenter as part of the environment. The required qualities are not usually present in the natural virus and, in the first passages on the chorioallantois, the genotype is in an adaptive valley. The genotypic change is gradual and, although the process has not been analyzed in detail, everything points to its being essentially similar to that worked out by Demerec for the adaptation of the staphylococcus to a penicillin-containing medium. Random mutations occur in all directions, occasionally toward a state better able to cope with the new environment. Such favorable mutants prosper at the expense of the original, and one eventually becomes the dominant form. From this, further mutants can arise which, in their turn, are still better fitted to multiply freely in what was initially an abnormal environment. Eventually, the species can be regarded as occupying a new adaptive peak.

In higher organisms reproducing sexually, the diversity of forms evolving from a single ancestral gene pool (species) may be due to the occurrence of gene mutations or of chromosomal modifications, *e.g.*, polyploidy, and the recombinations of the various genetic characteristics that exist within the Mendelian populations existing at any particular period. In microorganisms such as viruses and bacteria, mutation is the only important process so far demonstrably responsible for the development of new characteristics. Recombinations of qualities can occur under laboratory conditions, but it has yet to be shown that this is of any evolutionary importance. For all practical purposes,

we have to deal with clonal evolution, yet the end result is strikingly similar to that observed in the sexual evolution of higher animals and plants. There is the same diversity of creatures, and it is not a continuous diversity, but a discontinuous one. There is also the same strong indication of a hierarchical system of discontinuity. We must assume that the two types of evolution can lead to very much the same end result.

Probably, the outstanding feature of the evolutionary process in parasitic microorganisms is the unimportance of the individual. A few influenza-virus particles initiate infection in one individual of a susceptible human community, and an epidemic of some thousands of cases results. From the point of view of the virus, we have a series of precipitate population increases, followed by catastrophic destruction. In each individual infected, the peak population of virus particles probably exceeds 10^{10} , but it is certainly rare for even 10 of these to find opportunity for continued multiplication. When an active epidemic is in progress over a populous area, we might conceivably have 10^{17} virus particles in a viable state. A few weeks later, there may be no viable particles whatever in this particular environment.

The evolution of sex may be regarded as a means of retaining and recombining elements of mutational novelty in a more economical fashion than is possible with nonsexual organisms. Where numbers of individuals are virtually unlimited, mutation rate high, and generation time a few hours at most, there is no need for economy to conserve the useful mutation.

Two examples of an evolutionary process in viruses have come sufficiently within my own field of work to justify a little further discussion of the process of speciation. The first is in regard to the St. Louis, Japanese B, and West Nile group of encephalitic viruses to which we have recently added Murray Valley. In our hands, Murray Valley and Japanese B have only an incomplete immunological relationship of much the same character as between St. Louis, Japanese B, and West Nile, and I understand that Dr. Smadel's group are in general agreement.

Although probably too few strains have been studied from the various regions concerned to allow us to be dogmatic, it seems to me that, in this field, we may have something equivalent to the process of geographic speciation that occurs in higher forms. The endemic regions, at present, seem to be discontinuous, but there are some extremely interesting points about the Japanese B-Murray Valley relationship. Japanese B antibodies have been observed in Guam, and Murray Valley antibodies in North Queensland, so that there is a strong suspicion that viruses of the group may extend continuously along the margin of the western Pacific. A detailed serological study of the viruses from selected points along that arc might throw a lot of light on the process of virus evolution. I should consider that, with these viruses, serological character is a nonadaptive feature, the changes being accidentally associated with adaptive modifications for survival in the particular ecological complex—birds, mosquitoes, and climate—characteristic of the different regions.

What might be called temporal evolution may be seen in the changing character of influenza A. The stock strains SW15, WS, PR8 (or MEL), and

FM1 (or CAM) have antigenic qualities that allow very easy separation by anti H. A. tests. Were it not for the common complement fixation antigen, they might well be considered a distinct species.

Work done by Anderson in my laboratory on the hemagglutinin inhibition capacity of human sera from different epidemics showed much variation from serum to serum, but the general picture emerged that the majority of "broad" human sera contained antibody against infecting strain and against A strains that had been isolated in past years, but very little against "future" strains. We have put forward the hypothesis that influenza A virus survives in our current civilization of extensive and active movement all over the globe by a process of continually emerging serological novelty. Obviously, influenza has to move always through a partially immune population and serological novelty would be an advantage to survival except in isolated communities away from the main masses of population. The general experience of workers with influenza A is that there has been a continuing series of changes in serological character, WS, PR8, and FM1 representing convenient examples picked out from a changing continuum. Each new serological type seems to replace the preceding one very rapidly. The first A strain CAM was isolated in Australia in 1946. The epidemics in the northern hemisphere in January, 1947 were all of the new type. It is in line with this hypothesis that Mulder found that CAM showed a more definite antigenic relationship to PR8 than did FM1.

In this view, the serological character of influenza A (and probably B) is a highly adaptive feature that introduces a type of evolutionary change that has no clear analogies in higher forms, although, perhaps, a military historian might find parallels in the evolution of military weapons and tactics. Perhaps, a real analogy is to be found in the history of the wheat-breeder's struggle to produce strains resistant to rust. New physiological strains of the fungus always seem to arise to plague him.

All that I want to underline is that an evolutionary interpretation of the existence of a discontinuous range of virus forms is possible along lines that are based on the classical discussions of speciation in higher forms. It may be many years before a complete interpretation of the evolutionary development of the viruses is developed and accepted. I would not exclude the possibility that it may become necessary to consider some viruses as representing completely different orders of being from others but, for the time being, and for the purpose of nomenclature and classification, it is certainly expedient that we regard them as living organisms. I am not impressed with the contention that classification must wait indefinitely for even a beginning to be made. The fundamental techniques of virology are now soundly established and are sufficient to provide the solution, at least in principle, of the practical medical and economic problems raised by the existence of virus disease. I do not foresee any great spontaneous activity in fields of virology that will greatly advance the knowledge of systemic relationships. Advance will continue, as at present, to be dominated by the need to develop methods of control of virus diseases of practical importance, and by the study of the details of composition, the processes of infection, and multiplication in species specially favorable for labora-

tory study. Vaccinia and influenza viruses, the T-even group of dysentery-coli phages, and tobacco mosaic virus are the current favorites. It may be pessimistic so to believe, but neither of those directions of study seems likely to do more than add occasional sidelights on the problem of classification and nomenclature.

I think that a start on the work should be made now, and that the function of this monograph should be to provide guidance as to how that first step should be made, so that at least some progress can be consolidated before the next International Congress of Microbiology convenes.

My own attitude would be in line with the decisions of the Rio Congress, but might be put slightly differently. Taking, in the first instance, the viruses whose hosts are warm-blooded vertebrates, the logical procedure is to look over the whole range of characters presented by the various clones of such viruses as have been studied and recorded. Out of that diversity, we can see certain groups of viruses that seem much more closely related to one another than to any viruses outside of their own groups. Goodpasture, nearly 20 years ago, recognized this in regard to the pox viruses and his arguments have been given more force, since then, by the demonstration of the electron-microscopic appearance of the virus particles.

As a working rule, it might be suggested that viruses falling in one genus have approximately similar size and appearance in electron micrographs and, at least, one common functional characteristic. Species within the genus might be defined as containing all strains of similar serological structure.

That working rule, like any working rule in biological systematics, will be subject to the individual opinions of workers interested in the group being considered. Splitters and lumpers are as likely to appear amongst virologists, as amongst ornithologists, but this should not make broad agreement impossible.

There are some points of special difficulty with viruses that need discussion. I shall illustrate them only in terms of animal viruses responsible for human disease, but similar difficulties will probably arise in the other major groups as well.

The first is the mutability of viruses, particularly in relation to the frequent necessity of modifying the virus before it can be subjected to laboratory study. I have frequently pointed out that the "wild strains" of influenza A virus responsible for epidemic influenza will not multiply in the allantoic cavity, will not agglutinate chicken cells, and will not produce lung lesions in mice. All these characteristics are those of strains adapted to growth in the convenient laboratory animals.

In standard systematic work it is understood that, when a new name is given, one individual specimen is to be designated the type of the species and deposited in some suitable repository where it is available for subsequent study by other systematists. In bacteriology, the type culture collections fulfill this requirement. I realize that there may be differences of opinion on the point, but I should prefer to see definitive names attached only to well-studied viruses of which a certain clone can be maintained as the type specimen of the species.

The influenza viruses have been studied more closely than any other type of animal virus and, no doubt, the WS strain of Smith, Andrewes, and Laidlaw has much the strongest claim to be type strain of influenza A. In my laboratory, I have three strains, all of which, I am certain, are descendants of the virus that caused WS's attack of influenza in January 1933. The properties of the three are, however, extraordinarily different. One is neurotropic in mice, and two are capable of producing hemorrhagic death in chick embryos. The hemagglutinin of one is destroyed by heating to 52° for 30 minutes, that of another has to be heated to 67°C. All obviously differ greatly from the parent "wild" strain.

A definition of the species influenza A virus might, therefore, require a statement something like the following. Influenza A virus is the agent responsible for extensive epidemics of human influenza, including that in Southern England in 1933, from which the parent form of the type strain WS, now deposited in X collection of type viruses, was isolated. Strains of influenza A virus, when isolated and adapted to allantoic passage, have such and such characters in common with the type strain, and produce a soluble complement fixation antigen reacting with suitable antisera in the same fashion as the antigen produced by type strain WS.

Where a well-defined human disease has all the characteristics of a viral infection but the virus cannot be studied in the laboratory, the question of giving the virus a name is perhaps a rather unreal one. The only inconvenience that might be overcome is the difficulty of remembering what is the French or German for measles and German measles. Outside the human field, however, there are animal diseases such as the poxlike diseases of sheep and goats, or the immense range of plant diseases that have not yet been subjected to full comparative study for which accepted but provisional names would be a convenience. The suggestion that a group of provisional names for what have been termed Imperfectly Known Viruses should be adopted is a reasonable one provided machinery is available for the adoption of definitive names when relationships have been clarified.

There is already in existence a published classification of rickettsiae, animal, plant, and bacterial viruses, in the last edition of Bergey. I am certain that all virologists who have to deal with animal viruses agree that there are some serious misplacements of viruses in that classification, which, under any circumstances, would have to be corrected. On the other hand, I am rather attracted to Holmes's use of the names of traitors and derogatory epithets from the classics as generic names. It is going to be very difficult to find names with a direct indication of a distinguishing feature of a genus. The other alternative of attaching to each genus the name of some investigator who made an outstanding contribution to the knowledge of the group concerned is probably that most in line with current bacteriological practice. The difficulty of euphony tends to arise as in Holmes's *Miyagawanella*. Goodpasture's *Borreliota* is acceptable and the possibility of replacing the conventional "-ella" termination by "-iota" for viral genera compounded with proper names might be considered, but one can easily imagine that some appallingly inconvenient words, for

example: *Landsteineriota* for the polio viruses, would result, if the rule were followed. The form of a name, however, matters little once it has been accepted and used. Provided it is reasonably euphonious and has some association with the history or character of the group, anything will serve.

May I, in conclusion, attempt to summarize what I think are the problems on which this monograph should concentrate? In the first place, there is probably a danger that discussion of the classification of individual groups may turn too much on details that have no relevance to the general problem. Might I ask all contributors to consider to some extent at least whether the characters of their particular group can provide leads toward an acceptable general approach?

The problems for consideration are as follows:

(1) Is what may be called the Rio principle acceptable; *viz.*, that, for the time being, only those groups of viruses that have been extensively studied should be regarded as ready for treatment; or is it desirable that an internationally acceptable name should be attached to every type of virus that is distinct enough to require a name?

(2) If any Linnean or other nomenclature is adopted, the question of types for species and genus can hardly be avoided. I have already given an example in the form of a tentative definition of influenza A virus to indicate what extensive difficulties there are in relation to the maintenance of type clones of a virus and their relation to the "wild type." I can see no escape from the designation of a type strain for each valid species and of a type species for each genus. Others may feel that it mere pedantry to deny that measles virus, for instance, is a valid species, simply because there are no laboratory strains in existence.

(3) Can any agreement be achieved as to what are generic as against specific characters? To what extent must clones of virus differ to be accorded species rank? The old rule that the systematists should, as far as possible, disregard "recent" adaptive characters may be particularly sound in virology. Host range and virulence are clearly of little systematic value. Tissue preferences and capacity for transfer through an invertebrate host, reactivity with cell surfaces as in influenza viruses and bacteriophages, susceptibility to inactivation by physical and chemical agents, serological character, and, finally, size and electron microscopic morphology will all need assessment from this point of view.

(4) Should monotypic genera be allowable? In the field of animal viruses rabies is the outstanding example.

(5) Where there is a well-defined group, *e.g.*, the pox viruses, should poorly studied or rather distant types—swine pox and rabbit myxomatosis in the present example—be provisionally included or kept outside until further study clarifies the position?

(6) How far is it expedient to go in regard to higher level classification of the viruses, *i.e.*, in categories higher than genus? The most interesting of all the problems of classification, whether plant, animal, and bacterial viruses have a common evolutionary origin or whether, even within any of the three great

groups of known viruses, there are diverse evolutionary origins, is I think too remote from present-day knowledge to justify discussion in this monograph.

May I conclude by suggesting that there are two important reasons why we should go all out to make a start on virus classification?

The first is that any classification will act as a stimulus to virologists to try to better it and, in the process, to consider more deeply the evolutionary significance of differences between viruses (or any other groups of pathogenic microorganisms). I have held for a long time that such an approach is not only immensely absorbing as a mental exercise but also desirable for the practical understanding of such diseases as influenza and encephalitis.

The second is that an accepted classification and nomenclature will make it easier for those outside our own group of professional virologists—students, physicians, plant pathologists, and biologists generally—to understand our science.

From the very nature of the evolutionary process, any classification must be imperfect. I think, in the circumstances, we should strive for agreement rather than perfection.

In one final word, I should apologize for building this opening paper almost wholly around the problems of the animal pathogenic viruses. Nevertheless, apart from questions of origins, the same broad principles apply to all three groups, and I hope that what I have written is not wholly without application to plant and bacterial viruses as well.

CONCEPTS OF CLASSIFICATION AND NOMENCLATURE IN HIGHER ORGANISMS AND MICROORGANISMS

By Ernst Mayr

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It would be impossible to comprehend the unbelievably great diversity of nature without naming and classifying the units of which it is composed. Classification, of course, is not something confined to animate nature. We classify books in a library; we classify rocks or gems, laws and regulations, types of weather, in short, any variable phenomena.

All classification involves two steps. The first one consists of the definition of units, their description, and the finding of diagnostic differences between these units; in short, analysis. The second involves synthesis; namely, the assembling of the units into groups and their arrangement into an hierarchy of ever-larger groups. We must understand this process of classification if we are to arrive at a sound nomenclature.

What is the basis of our current system of zoological nomenclature?

Systems of Nomenclature

Names are recognition symbols. In biology, they are an international language that makes the repetition of detailed descriptions unnecessary. Names for organisms have existed long before scientific names were given. Even the most primitive tribes in Africa, South America, or New Guinea have vernacular names for animals and plants. They are usually uninomial, expressing distinction, such as skunk, elk, robin, or flicker. Beginnings of a binomial nomenclature, consisting of a combination of a group name (generic name) with a specifying name (specific name), are also sometimes found not only among pre-Linnean authors but even among primitive people. It was, however, Linneus who made it the basis of a consistent system of nomenclature, that of binomial or trinomial nomenclature.

Every animal or plant has a scientific name according to this system, which consists of two words. The house sparrow, for instance, is *Passer domesticus*. *Passer* is the generic and *domesticus* the specific epithet. The precise significance of binomial nomenclature was not entirely clear to Linnaeus nor to most of his successors. In fact, it is not clearly understood by many of our contemporaries. The two names of which a scientific name is composed have actually opposite functions. The specific name expresses distinctness; the generic name relationship. It is evident then that binomial nomenclature, in order to be meaningful, must be based on sound classification. Sound classification, in turn, is founded on a thorough knowledge of the units which are to be classified, and improvements of classification are ultimately attainable only through improvement of our knowledge of these units.

The history of all classification, whether dealing with inanimate objects or with organisms, shows that early attempts of classification are based on superficial similarities and very often on single characters, while all improvements of

classification are due to an ever more deeply penetrating analysis and a broadening of the basis of classification by including more and more characters. The soundest classifications are those built on the greatest possible number of clues. Reciprocally, it can be stated that, in sound classifications, there is usually a fair concordance of the various characters. The question of the reliability of taxonomic characters is an important one, but too broad a subject to be pursued further in this connection. I must refer to more extensive treatises.

The problems of nomenclature that are confronting the virologist are whether or not the time has come to apply binominals to viruses, and, if so, on what principles to base such nomenclature. The knowledge of the higher animals was already far advanced when Linnaeus introduced the system of binomial nomenclature in zoology. In 1758, when this was done, nearly all of the more common species of mammals and birds of Europe had already been precisely defined. It is well to remember this when attempting to apply the system of binomial nomenclature to such poorly known organisms as the viruses are.

The second step, the synthesis of the lower categories (the species) into higher categories (genera, families, and so forth) has lagged far behind the first one. Many of the higher groupings are still very dubious. Although the last North American species of birds was discovered in 1889, we are still in doubt as to how many genera of North American birds to recognize, and are completely in the dark with respect to the delimitation and relationship of families. We may conclude from this that the application of binomial nomenclature requires a fairly advanced knowledge of the basic units, but is not too much interfered with even by fairly extensive ignorance of the arrangement of the higher categories.

A precise knowledge of the units to be classified is essential but not enough. What is also needed in biological classification are classifying principles which help the systematist to devise sound classifications.

Two facts more than any others have led to the chief conceptual improvements of our system of biological classification. The first is the principle of evolution. It is now realized that the similarity of organisms and of groups of organisms is not a freak of nature, but is due to the fact that similar species and genera are descended from common ancestors. The "natural system" of the taxonomist then reflects phylogeny. In fact, some authors have gone so far as defining taxonomy "as the scientific classification of the different kinds of living organisms according to the proved or inferred phylogenetic relationships." This concept is based on the belief that organisms that have descended from the same ancestor will have more characters in common with each other than with any other kinds of organisms. It is now known that this is not always the case, since selection pressures may lead to a considerable divergence from the ancestral type. For instance, birds and crocodiles are phylogenetically closer to each other than are crocodiles and turtles, or crocodiles and lizards. Yet, the conquest of air by *Proavis* has led to such a dramatic reconstruction of the avian system that birds are now much more different from crocodiles than the latter are from other reptiles.

The theory of evolution has had its main effect on the *synthetic* processes of classification, the definition of groups, and their arrangement in an hierarchy of categories. A different biological concept has greatly influenced the results of the *analytical* stage of classification; namely, the definition of the units of the taxonomist, which he calls species. I am referring to the concept that the process of sexuality leads to a genetic integration of natural populations into species.

Modern studies by systematists, ecologists, and population geneticists have made it abundantly clear that the species is a unit as important and meaningful in biology as the cell, or as is the atom in physics. In fact, the species occupies a central position in the hierarchy of organisms. In order to understand the true significance of species, it is necessary to say a few words about the biological meaning of sexuality. The significance of sexuality is genetical. Sexuality permits recombination of gene complexes and thereby provides an inexhaustible store of genetic variability. Modern researches have shown conclusively that the most objective property of species is perhaps the gap between different species. It is the place where gene exchange is interrupted. Species then can be defined as populations that are separated from each other by a reproductive gap. We shall return presently to the definition of species.

Sexual reproduction is *par excellence* characteristic of higher organisms, particularly of the higher animals. They nearly always live in a generalized variable environment with a great complexity of external conditions. High genetic variability is a great advantage under such conditions. Although the more extreme variants will be eliminated by the environment in each generation, the total variability will be continuously restored by recombination as a result of the sexual process. The greater the variability, the greater the opportunity to utilize the variability of the environment.

It appears that conditions may arise in nature which may place a selective premium on the temporary abandonment of sexual reproduction. One such situation is when an empty niche must be filled rapidly, and selection pressure is very much reduced. This is true, for instance, for fresh-water plankton which arrives in previously vacant lakes; or for plant lice which, in spring, have suddenly available an inexhaustible food supply on freshly developing leaves. The production of parthenogenetic females, each of which again produces only females, will lead to a much more rapid filling up of the niche than the production of 50 per cent females and 50 per cent males.

In view of the importance of interbreeding populations for the definition of species, it is evident that information on the presence or absence of sexuality is of vital importance to the taxonomist. It is precisely with respect to *this* subject, however, that information is still very deficient on viruses. What little information there is suggests that sexual processes may be widespread, if not universal, among viruses, but that there is often a temporary abandonment of sexual reproduction.

Genetic recombination, that is, sexual reproduction, has been recorded up to now in only a few viruses. In the cases in which it was seriously looked for, however, it was nearly always found. The assumption of the widespread occurrence of sexuality in viruses is backed also by the following consideration.

Virus strains fall normally into well-defined groups: Influenza A, mumps, *etc.* If reproduction was strictly asexual, one would expect mutation in the independent strains to have such a pronounced centrifugal effect as to obliterate eventually all traces of groups. The existence of groups indicates that occasional gene exchange between diverging conspecific strains prevents the dissolution of the groups. The frequency of recombination may be very low. The chance that it will be discovered, if it occurs in one of 5000 generations, is very small. Furthermore, the occurrence of sexuality may depend on very specific environmental conditions as in parthenogenetic higher animals or on multiple simultaneous infections.

In view of the scarcity of available information, however, it would be premature to study the ecology of this potential "alternation of generations," as we may call it. There are various factors that might place a selective premium on temporary asexuality. If a new host is invaded, it is highly advantageous for the virus to reproduce at maximum speed, before immunity reactions develop. This would favor temporary asexuality. Additional factors, however, may play a role. Viruses, being adapted to cells of a single host, live in a much more uniform environment than free-living higher organisms. Great genetic variability might be actually a disadvantage with them. As soon as a superior, that is, highly viable, gene combination is found, it will be advantageous to reproduce this superior gene combination asexually rather than to try to improve it by genetic recombination at the risk of destroying it. It is very probably that microorganisms have a much less complex genetic system than higher organisms, that the gene complexes are less well "buffered," and that every mutation affects the phenotype more conspicuously than in higher organisms. If so, there would be a premium, in such a system, on the reduction of sexual reproduction and on a rise in the rates of growth and reproduction.

It is possible that, in such a system, mutability may in part take over the function of recombination in higher organisms. Considering the enormous population size in microorganisms and the high number of generations per time unit, even a low mutation rate can provide an amount of variability that might offer all the needed material for selection in a slowly changing environment.

For all these reasons, it is evident why there is so much (temporary) abandonment of sexual reproduction among microorganisms. The classifying taxonomist then will have to deal both with sexual populations and with asexual strains or lines. We must keep this fact clearly in mind, when we try to place microorganisms into the categories which have been defined for sexually reproducing higher organisms.

The Meaning of Categories

The taxonomist classifies his material by arranging it into categories. As stated above, the species is the basic of these categories, and it is therefore necessary to say a little more about the meaning of the category *species*. The species concept goes back to Plato, to whom species meant "kind." This concept still lives outside of biology, as for instance when a mineralogist speaks of "species" of minerals. From this original species concept arose that of the