The Twelfth Symposium of

THE SOCIETY FOR GENERAL MICROBIOLOGY

*edited by*

G. C. AINSWORTH & P. H. A. SNEATH

# MICROBIAL CLASSIFICATION

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# EDITORS' PREFACE

That taxonomy is a fundamental branch of microbiology has always been recognized by the Society for General Microbiology. In September 1954 'The principles of microbial classification' was the subject of a one-day Discussion Meeting at Reading;* recently a Microbial Systematics Group has been established within the Society for the increasing number of members interested in taxonomy; here microbial classification is again reviewed.

Microbiology is not the sole preserve of bacteriologists, and while bacteria occupy a central position in this Symposium an effort has been made to consider the taxonomy of all the major groups of micro-organisms against a background sketched in by a zoologist and a botanist experienced in the taxonomy of larger organisms.

Each contribution is self-contained, but all are interrelated. Some, such as those on protozoa and algae, comprehensively survey the taxonomic treatments of single groups, some contrast different approaches to the taxonomy of one group, while others discuss the application to different groups of one taxonomic approach. This volume therefore reflects facts and uncertainties of present-day microbial classification, both theoretical and practical.

Help and advice from contributors and from other members of the Society in the preparation of the three Appendices is gratefully acknowledged.

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* For a report see *J. gen. Microbiol.* **12**, 314–86, 1955.

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# THE EVOLUTION OF TAXONOMIC PRINCIPLES

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The purpose of studying the history of a scientific subject is to cast light on its present state. It is only too easy in any period to hold beliefs which are unformulated because unquestioned, and which are an actual hindrance to a more complete view of the subject. Perhaps there is no part of biology in which this is more true than it is in taxonomy, which for so long has progressed by a combination of tradition and rule of thumb.

Taxonomy is the science of classification (or, more broadly, arrangement) as applied to living things. Almost every advance in biology has had its effect on classification—nearly everyone has views on how things should be classified, and what are 'really' related and what only superficially similar, in biology as in every other science. Moreover, some sort of arrangement is inescapable for organizing our facts about the bewildering diversity of living things; and a nomenclature is equally essential as a quick and accurate method of reference and communication.

It is unnecessary for our purposes here to go back beyond Linnaeus, who is not only the accepted starting-point for nomenclature, but perhaps the most typical member of that school of taxonomy which began with Aristotle and his contemporaries and whose theories still influence taxonomy today. Yet very much of the so-called Linnean system of taxonomy as used today would be strange to Linnaeus, and most of what has been inherited from him is of rather doubtful value.

Linnaeus's principles of taxonomy can be summarized as follows (for a more detailed discussion see Cain (1958) and references therein).

(i) There are distinct *kinds* of living things without intermediates, each with its own peculiar characters or combination of characters. Each is separately created (or, as Linnaeus came to think later, evolved by hybridization from a limited number of originally created forms), breeds true, seldom, or only locally, hybridizes with others in the wild, and has a distinct role to play in the Economy of Nature. These are the *species*.

(ii) The species are constituents of higher groups which are themselves distinct and separate, each with its peculiarities, and these again are members of yet higher groups, and so on up to the group of all living things.

(iii) The best method of arranging living things is to find out what they 'really are', what is their *essential nature*, and to *divide* all living things according to the modifications of this essential nature. Each division can itself be subdivided according to modifications of its essential characteristics, and so on down to the least divisions, the *species infimae* in the terminology of Aristotelian logic, which are Linnaeus's taxonomic species.

(iv) The most important characters for doing this are therefore the most essential ones, those that have the greatest influence in making the organism what it is, those in short that have the greatest *physiological importance*.

(v) The arrangement that most successfully carries out these principles is the most *natural* (because it expresses the *natures* of the things arranged). An arrangement that does not express the natures is an artificial one, which may be very useful for some special purpose. It may, for example, group things so that they can be readily identified, associating them in groups definable by some obvious but often trivial character which springs to the eye but does not indicate the 'true nature'.

Linnaeus's nomenclature accords closely with his theory and practice. Since, according to him, the species are the ultimate taxonomic units, then each should be given a distinct name. But, in practice, it was often difficult to name plants down to the species; and the higher groups of plants were not in his time generally agreed on, since most text-books used frankly artificial systems of arrangement, sometimes based on the leaf, sometimes on the corolla, sometimes on other parts of the plant, or on vague groupings intended to be natural. The genus, therefore, had for him an immense practical importance. All systematists, he thought, should know their genera by heart (he believed this to be perfectly possible) and then they would know at once with which kind of thing they were dealing. Consequently, he named genera for the easiest possible reference and the greatest memorability by giving each a single word which is a proper name. The species he named by a *differentia*, to follow the generic name; but his *differentiae* were often in effect lines of keys defining each species within the genus by stating some of their peculiar characters or character-combinations. As this meant that they could be up to twelve words long, and moreover, as they were liable to alteration if a new species was discovered, he produced also a single word, the *trivial epithet*, for each species, which he regarded as a mere catchword—in fact he never even bothered to give rules for its formation. It is this trivial name which has survived as the name distinguishing each species within a genus, since the *differentia* has become a line in what is explicitly a key, and has become a diagnosis in any more extended treatment of the group.

Linnaeus's principles of classification are based on the theory of Logical Division worked out by Aristotle, which held the field until the beginning of this century (later in some quarters) as the only good way of arranging anything. It was a most praiseworthy attempt to classify things by what they 'really are', and to avoid being misled by mere superficial resemblance. It failed because it was essentially deductive but was applied indiscriminately to situations where only inductive treatment was possible and never provided adequate criteria for deciding the meaning of the phrase 'what things really are'. A more detailed treatment of it is given by Cain (1958).

Logical Division can best be exemplified in such a subject as geometry. We can define exactly what we mean by a term such as circle or plane triangle. Then its definition states its *essence*—what it must be to be a circle, or triangle, at all. Any other attributes which a particular circle may have (e.g. its size, or the colour of the pencil used to draw it) are, in the technical sense, *accidental*. They can vary, without in the least causing it to be less or more a circle. But the number of sides of a plane triangle cannot vary, by definition. Furthermore, everything that follows rigidly from the essence or definition is a *property* of the circle or triangle, or other figure, always and necessarily possessed by every figure with that particular essence—for example the sum of the internal angles of any plane triangle must be 180°. Such constant characters would be of the utmost value in identifying the essential nature of a given entity, supposing that this were not already known. And since there are many sorts of triangle, we can divide the genus triangle into species by considering what is the essence of plane triangularity, and in what ways that essence can be expressed. If plane triangles are defined as plane figures bounded by three straight lines, then the logical choice for dividing them up into groups would be the proportions of these lines—and the usual division is into equilateral, isosceles and scalene. This is an excellent example of Logical Division; the essence of the kind (*genus*) of thing under consideration is first determined, and then the different forms (*species*) in which it can manifest itself are so determined that (*a*) they are mutually exclusive, with no overlapping classes, and (*b*) taken together they exhaust the genus, so that no species has been omitted. This sort of division was considered as excellent by Aristotle. We can easily see from it why he put immense emphasis on determining the essences of things, dividing up according to these essences, and disregarding mere accidental characters.

But suppose we try to apply this sort of procedure to living things. We can define an animal, but only descriptively. We do *not* know its essence; we cannot decide what are properties and what only accidentals. Certainly those characters that vary greatly within a group (from individual to individual within a species, or from genus to genus within a family, for example) must be accidental in that group. We might well think, by analogy with Logical Division, that those characters which are constant in a group, as far as our experience goes, are all properties. But this cannot be demonstrated; some, perhaps many, may be only accidentals that happen not to vary within our limited experience. Until Australia was discovered, it was possible to believe that whiteness is an essential character of swans (and therefore if a bird were not white, it could not possibly be a swan), but the discovery of black swans revealed colour as an accidental in this case.

Nevertheless, there has always been a considerable practical value in working out what characters are constant in a group, in order to define it. A horse is first shown to each of us in infancy by someone pointing to an example and pronouncing the name 'horse'. But the next one pointed out may be a different colour, or size, or with a longer tail... and so on. What is it that defines a given animal as a horse and not a cow? All the characters just mentioned vary greatly. The horsiness of a horse does not reside in the beast's colour, but in a multitude of anatomical and other characters found in combination in all horses. Such constant characters could be considered as properties, and a collection of them could be regarded as a definition of the essence, comparable with the definition of plane triangles, so that even in biology, the revered procedures of deductive thought could be approached. But in fact, such definitions are not of essences and allow of very little safe logical deduction. They are summaries of observations, useful for the definition of groups, but not the analysis of kinds, essentially inductive, and liable to upset by further discovery. They are invaluable for defining terms by means of which we can make sure that we are talking about the same sort of animal as someone else; and they are very useful summaries, making our classifications as concise as possible, and so the more easily scanned and (if necessary) memorized. Consequently, they have remained in use; but, unfortunately, they carried for centuries a prestige which was not theirs. The man who really knew what his subjects were and could reason about them deductively was obviously far better informed and more competent than he who could only group together those of his subjects that seem alike on mere observation without reasoning, an activity stigmatized by A. P. De Candolle as 'blind groping' (Cain, 1959*a*). Anyone, therefore, who could claim that he had definite principles on which animals or plants *must* be distributed into groups must be a better taxonomist than a mere grouper.

But, in fact, this blind groping was the only scientifically honest procedure. The logician Joseph (1916) has put it very clearly in relation to organic beings. 'If species were fixed: if there were in each a certain nucleus of characters, that must belong to the members of any species either not at all or all in all: if it were only upon condition of exhibiting at least such a specific nucleus of characters that the functions of life could go on in the individual at all; then this nucleus would form the essence of the kind. But such is not the case.... There may be deviation from the type, to a greater or lesser degree, in endless directions; and we cannot fix by any hard-and-fast rule the amount of deviation consistent with being of the species, nor can we enumerate all the points, of function or structure, that in reality enter into the determination of a thing's kind. Hence for definition, such as we have it in geometry, we must substitute classification; and for the demonstration of properties, the discovery of laws'—i.e. the inductive determination of regularities from actual observation of as many instances as possible.

In the period from Linnaeus to Darwin, many workers had tried to find the 'natural classification', that which was based on the true natures of animals and plants (Cain, 1959*a*, *b*). Almost always they had tried to do so on fixed *a priori* principles, in imitation of the deductive sciences, but often these would separate things which were so clearly related in every way that it was obvious that they must be kept together. A famous early example was the division of plants into woody and non-woody, on Aristotelian principles, which associated leguminous trees, for example, not with leguminous herbs, but with all other trees,—a ridiculous grouping, and recognized as such even before the time of Linnaeus. Merely as a result of taxonomic practice, it was becoming more and more evident that one could not lay down fixed principles on which to work, because they produced absurd results in some group or other; or some character of no importance according to the principles adopted was found to be of the greatest importance in defining a particular group—and therefore must really be important after all, which meant that the principles must be wrong.

The reason why it took so long to unmask the inadequacy of *a priori* division in biology is rather remarkable. Taxonomists were arguing in a circle without knowing it, and using one half of the circle as a separate argument from the other, which confirmed and strengthened it, thus increasing their confidence in their results. Two quite distinct and equally important taxonomic activities, at least as far as bi-sexually reproducing forms are concerned (which were the only forms considered until very recently), are the sorting of animals into different species, and the grouping of these species into higher and higher groups. The first involves such questions as 'Does this specimen belong only to a seasonal form, or a geographical race of an already known species; or is it a somewhat abnormal individual of one, or have I discovered a new species altogether?'—that is, a separate entity, genetically distinct from all others, and with its own mode of life. It leads to the distinguishing of the different *units* of animal life, so to speak. Its questions, as far as living things are concerned, can usually be settled by breeding experiments of a certain sort. The second activity involves such questions as 'Is the cheetah sufficiently different from the other great cats to require a group by itself, equal in rank to that containing all the others?' or 'Are the whales fishes or mammals?' or 'What animals should be put as the closest relatives of the common fox?' Such questions can never be settled decisively by experiment. They involve the weighing up of a large number of characters in all the forms considered, and some sort of overall comparison of similarities and differences against arbitrary standards. Such grouping is very readily done in an imprecise fashion by the human mind—anyone can 'see at a glance' that stoats and weasels and martens are far more like one another than like foxes and wolves. Such natural groupings—not according to natures in the Aristotelian sense, but according to mere 'blind groping'—have always been recognized. They are the real basis of early classification, and in fact, without them, classification could not even start. How was it that Cuvier, for example, could state what are the important characters of animals, and then proceed to distribute animals according to them on *a priori* principles? He could only do so because a natural group of animals (in contrast to plants) had *already* been recognized; after its recognition, the characters common to all animals could be sorted out from those possessed by only a few (which might then be used to define a natural subgroup of animals, or might be found to crop out sporadically in various natural subgroups, and have no diagnostic value). But if these characters had already been singled out as important on a natural grouping, there was no point in proclaiming that they must be important on principle, since the 'principle' was no more, very often, than a restatement of the fact that they were already found to be important. Nevertheless, many taxonomists including Cuvier (Cain, 1959*a*) *deduced* the physiological importance of various characters, and then claimed that as they could observe these characters to be very constant through large groups, they had confirmed their reasoning by observation. The question never asked was: 'How did we get our generally accepted groups of animals in the first place?', and the answer, which would not have been admitted because of deductive reasoning's high prestige, was 'By what you have called blind groping'.

Darwin and a few others were fully aware of the uselessness of the *a priori* principles that had been used. In the *Origin of Species* Darwin wrote, 'We must not, therefore, in classifying, trust to resemblances in parts of the organization, however important they may be for the welfare of the being in relation to the outside world [since this would group, for example, whales with fishes, or mice with shrews]. Perhaps from this cause it has partly arisen that almost all naturalists lay the greatest stress on resemblances in organs of high vital or physiological importance. No doubt this view of the classificatory importance of organs which are important [physiologically] is generally, but by no means always, true. But the importance for classification, I believe depends on their greater constancy throughout large groups of species; and their constancy depends on such organs having generally been subjected to less change in the adaptation of the species to their conditions of life...no one will say that rudimentary or atrophied organs are of high physiological or vital importance; yet undoubtedly, organs in this condition are often of high value in classification...'. In this he was perfectly right. At long last, deduction in imitation of the mathematical sciences was recognized as inapplicable in taxonomy, and pure observation of what characters were common within natural groups could be taken as the basic procedure for the second taxonomic activity. A. P. de Candolle had gone half-way to recognizing this fact (Cain, 1959*a*).

But Darwin himself had theoretical principles which could be applied to taxonomy, and he proceeded to apply them. There was an unsolved problem in taxonomy, which on the theory of evolution was immediately explicable. Rudimentary organs had always been a puzzle. Aristotle himself could do no better than suppose that although Nature could produce animals of the same general plan but modified to lead different lives, she could not modify such a plan in any really essential features; and therefore rudiments of such features must always exist in the most modified forms 'for a token' of what the plan was in its unmodified state. In later times, a very similar interpretation was used. The rudiments served to show the main idea which the Creator had used in designing the modified forms. In tracing out these ideas, one was following the plan of creation. And many moralists pointed out how marvellous in ingenuity the Creator had been, to produce such infinitely diverse variations of a few themes and build up from them the complete Economy of Nature. This was a sublime interpretation. It graced with the beauty of holiness the study of natural history. But it was a subject for contemplation only, and gave no practical help to Science. Why should the Creator leave these tokens and rudiments? Moreover, if it was true that every sort of living thing was created perfect for its own role in the Economy of Nature, how was it that one did not find the same sort of animal performing the same service everywhere on the globe where that service could be performed? Why was it, for instance, that the place of the little auk as a small marine diving fish-eating bird was taken in the South Atlantic by a quite unrelated bird, the diving petrel, or that the large grazing mammals in Africa were antelopes but in Australia—in almost identical country—were large kangaroos?

The answer was obvious on the theory of evolution. The local stocks had been modified in each great region to occupy the available niches, and often they still bore the traces of their ancestral conditions. The reason why a natural group of vertebrates, or molluscs, or insects, could be recognized was simply that each did consist of variations on a single theme, but the theme was set by the ancestral form from which all the variations had been evolved by adaptation to different modes of life; the rudiments were there not as a token of the limited powers of Nature, nor of some mystical theme in the plan of Creation, but simply as relicts of a more ancestral condition. Community of descent, as Darwin said, was the bond between the members of a natural group.

This interpretation of the classification of living things into a hierarchy of groups was so convincing and so convenient that it was accepted unreflectingly by all the people who accepted evolution. At long last, the difficulty over rudimentary organs was disposed of; and taxonomists could go on exactly as before, merely interpreting their natural groups as groups which had a common ancestor. They had been tracing the course of evolution without knowing it, and needed only to acknowledge the fact.

But one may well wonder whether this simple equation of the classification with an evolutionary tree is not too simple. Many of the groups recognized in Darwin's day were badly known, and divided up on some principle or other rather than into natural subgroups. A complete overhaul was necessary before the equation was made. There was, moreover, one difficulty far more serious than this. Darwin had admitted, in his examples of the little auk and the diving petrel, the whale and true fish, the mouse and the shrew, that convergence could occur, by adaptation to the same, or a very similar mode of life. He never discussed convergence with any thoroughness and no example of it appears in the (hypothetical) ancestral tree he drew to illustrate his views on descent and classification. He appears to have assumed that convergence could never go so far as to produce virtually identical forms from different stocks. Now it may well be true that conditions over the face of the earth vary so much from place to place and from time to time that the chances of two very different stocks being continuously modified in the right directions for so long that they become virtually identical, are exceedingly small. But suppose that the stocks are already closely related and very similar: they might very well come to occupy the same mode of life (in different regions) by quite a small modification of each. And suppose further what is far more likely to be true than not, that we have no good fossil record of the group, how should we know that the very close resemblance between the end-products is only in part due to a common proximal ancestor, the remainder being convergent? But a classification which is professedly based on the course of evolution must always distinguish convergence from ancestral resemblance.

This difficulty has never been satisfactorily cleared up (Cain, 1959*a*, *b*). For large parts of the animal and plant kingdoms, our best mode of classification is still by 'blind groping', by putting together those things that resemble each other most, all their characters being taken into consideration. In such groups we may *believe* that most are truly phyletic groups as well, each stemming from a common ancestor, but we have no way of checking how far this is true, and generalizations about the course of evolution which are based on them are insecure. For other groups, however, the fossil record is good enough to allow us to see a great part, if not all, of the course of evolution in them, and they afford our only firm basis for its study.

By equating taxonomic with ancestral relationship, Darwin, like Cuvier, adopted two criteria of the importance of characters. On the one hand, he said that those characters common to large groups (i.e. *natural* groups, although he did not say so explicitly) are more important than those common to groups containing little diversity. This is always right if only natural groups are to be made. But he also said (*a*) that those least likely to have been modified in relation to particular modes of life will be more important in showing ancestral affinity, and (*b*) that they can be recognized because they will be the most nearly constant ones within a natural group. But this assumes that natural groups are always phyletic or, in other terms, that convergence is never so great as to obscure or outweigh ancestral resemblance even in poorly known groups. He did not commit the earlier error of arguing in a circle. His principles of evolutionary importance were not derived from a pre-existing taxonomy, but from the results of artificial selection and from the study of heredity, variation and ecology. This is a point worth emphasizing. In many elementary text-books of biology, classification