

Principles and Practice of Bacterial Taxonomy— a Forward Look

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SUMMARY

Taxonomy is divisible into three parts: (1) classification, (2) nomenclature, (3) identification. There are rules of nomenclature but none for classification or identification. Six principles are postulated for classification of bacteria and three ways of making identifications are discussed. Both classification and identification depend on characterization of the bacterium, but each makes different use of the individual feature. In classification equal weight is given to each independent character; in identification characters are weighted, some as important (distinguishing), others less so. Exception is taken to the retroactive application of the rules of nomenclature, and the unrealistic starting date (1753) of bacterial nomenclature is criticized. Names act merely as labels and it is suggested that a sequential code should be used, not only as a substitute for a name, but as a means of conveying information about the characters of the organism.

INTRODUCTION

Systematics is the study of multiple items, units or individuals with the aim of finding common factors and differences; lines of cleavage are made so that the like fall on the same side of the dividing line, and the unlike on the other. Biological systematics bears the special name taxonomy, and the subject can be subdivided into three sections.

(i) *Classification*, the orderly arrangement of units into groups of larger units. A simple analogy can be found in a pack of cards; the individual cards can first be sorted by colour, then into suits. Within each suit the cards can be arranged in a numerical sequence, and the face cards placed in some order of seniority.

(2) *Nomenclature*, the naming of the units defined and delineated by the classification. In the example of cards, the face cards are given names and more than one name, for example, jack or knave, may be given to the same card.

(3) *Identification* of unknown units with known units of the classification developed in (1) and bearing names given in (2).

These three facets, or the trinity that is taxonomy, are to some extent interdependent, but in an orthodox scheme they are considered in the order given above. It is arguable whether the hen or the egg came first, but since the end of the nineteenth century bacteriological ethics have demanded that we should not name a bacterium before we have allotted it to a unit in an orderly classificatory system. This is not only ethical but common sense, for we cannot identify an organism until

the preparatory work has been done; this means that identification depends on adequate characterization, description and comparison with published work.

The end result of a classification is often presented in a deceptive form, deceptive because we read downwards and it appears that the scheme starts by taking one large group, say Bacteria, and breaking it down progressively into small and smaller groups; this is a hierarchical system (Fig. 1). In fact the converse has occurred; the units have been built up from individual isolates, similar isolates have been united as species, similar species as genera, and so on. Represented diagrammatically, this build-up looks like a tree (Fig. 2), but when we describe it we always invert the tree so that it looks like a genealogical chart (Fig. 1).

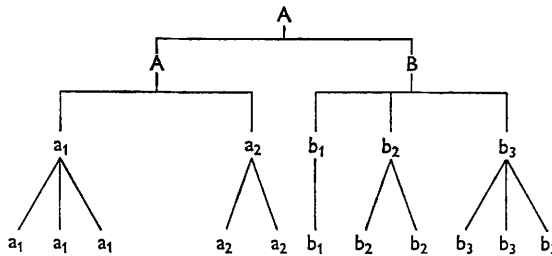


Fig. 1. A hierarchical system shown in the form of a genealogical table. Division of a large unit A into smaller subunits A and B, with further subdivision into sub-subunits (a_1 , a_2 , b_1 , b_2 and b_3) made up of individuals.

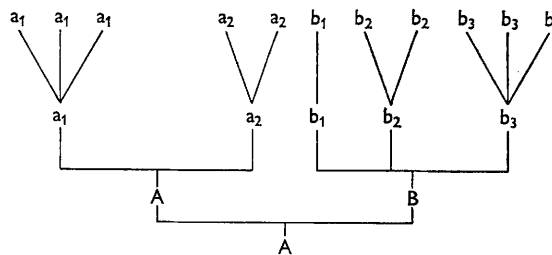


Fig. 2. A 'tree' which shows how groups of similar individuals are united as larger groups, which themselves are combined to form still larger groups.

PRINCIPLES OF BACTERIAL CLASSIFICATION

I. Purpose

The first principle is that there must be a purpose or reason for making a classification; it follows that there can be several classifications of the same objects, each scheme being created for a particular (and usually different) reason.

II. Subdivisions

The subdivision of a large unit does not follow any law; for example, the subdivisions do not need to be of equal size, or to be equally spaced. The philosophy of taxonomists themselves is reflected in the subdivisions they make. They can be subdivided (or classified) into clumpers and splitters; again, the division is not an equal one, neither is it clear-cut; on analysis it appears that when bacterial taxo-

nomists deal with their own group they are splitters, but when surveying bacteria as a whole they are clumpers of those organisms they know least about.

The first two principles of taxonomy give the taxonomist complete freedom to make his subdivisions as he will. It follows that it is unlikely that two workers will have identical reasons for making a classification, or will agree on all the lines of cleavage.

III. Uniformity of units

The third principle is that there should be some parallelism in the subdivisions of the hierarchy, but because of the subjectivity of taxonomy this principle is seen as much in the breach as in the observance. It is observed in the subdivision of the pneumococci into serological types dependent on the chemical nature of the capsular polysaccharides, and of *Streptococcus pyogenes* by the M and T surface proteins. It is breached when we compare the serotypes of streptococci with those of *Salmonella* which some regard as species and others (Kauffmann, 1963a) as units above species.

IV. Circumscription

Precision of definition is the fourth principle of classification. The boundaries of each unit must be defined; so that they are clearly recognizable by other workers. Thus, in the second half of the twentieth century the definition of *Escherichia coli* must be more than a Gram-negative rod that produces acid and clot when grown in milk; on the other hand, all the antigenic details do not need to be defined; indeed, a definition based solely on antigenic structure is as inadequate and unacceptable as any made by Escherich and his contemporaries.

V. Characterization

A unit cannot be defined until it has been characterized, which means until we have studied the morphology (including cytology), physiology, chemical make-up, enzymic constituents, genetic and other factors. The detail yielded by these studies will vary with different organisms, but the aim should be to produce as much information as possible; from this we look for pairs of correlated characters. There has been, and still is, much argument about the value of different characters and this point will be discussed later (see Principle VI). We often speak of 'adequate characterization' but seldom say what we mean by that term; one imagines that to a cytologist a characterization without details of cell walls, membranes, septa and nucleus would be inadequate, and that a serologist would regard a description that did not include antigenic structure as quite unacceptable. A characterization cannot be adequate unless it is fairly comprehensive; thus the descriptions of *Mycoplasma* species (PPL0) are inadequate because we know so little about their characters; in the same way, but to a lesser degree, the characterizations of *Neisseria* species are inadequate because these organisms may not grow in media developed for the characterization tests used for most organisms. Among the viruses characterization of the organism (if viruses are organisms) is limited, although cytopathic effects can be determined and may become part of the virus characterization.

The adequacy of characterization of a bacterium is a reflexion of time; it should be as full as modern techniques make possible. Unfortunately, one now regarded as adequate is likely, in ten years time, to be hopelessly inadequate!

VI. *Weighting of characters*

The weight to be attached to different characters is the sixth principle of classification; this is so debatable a subject that it requires more detailed consideration than we have given to the other principles. The early bacteriologists used the minimum of features in describing their organisms and, as the bacteria most studied were thought to cause disease in man or other animal, the organism was named after the disease. There was little attempt to create a systematic classification or nomenclature; the greatest stress was placed on morphology and, because only few characterization tests were then available, on a few simple cultural characters such as growth in various media, liquefaction of nutrient gelatin, and the changes induced in milk. By virtue of the length of time for which they have been used, these characters have assumed an importance out of all proportion to their usefulness. It was also found that certain characters easily shown by simple tests (for example the ability or inability to produce acid from lactose) seemed to be associated with certain bacteria; some of these bacteria (lactose-fermenters) were found in healthy people, others (non-lactose-fermenters) mainly in the sick. The tests then became important and the characters they revealed were regarded as important. Thus there developed a climate in which tests (and characters) were regarded as important or not important; in general the important ones were those that we should now call 'distinguishing', and they still retain all their importance in identification. But as classificatory criteria they are now under a cloud.

Adansonism. Sneath (1957 *a, b*) drew attention to the theories and ideas of the French biologist Adanson (1727–1806), and applied his principle that all features had equal merit in making up the characterization of the whole to the characters of chromobacteria, in which Sneath showed that there were two major subgroups. The analysis was made easier by using a computer, and an extension of the 'electro-taxonomy' to a wider range of bacteria showed that the principles enunciated by Adanson were applicable to the classification of bacteria (Sneath & Cowan, 1958). It was a tribute to the work of the older taxonomists that a classification made by giving equal weight to all characters produced results which, by and large, confirmed the empirical classifications that have been used for so long, such as those proposed by Winslow *et al.* (1917, 1920), *Bergey's Manual* (1923–57) and *Topley & Wilson's Principles* (1929–64), to mention but a few.

Few taxonomists would now deny that Sneath made a most valuable contribution to bacteriology when he drew our attention to the principles of Adanson, for he was not only able to develop numerical taxonomy (Sneath & Sokal, 1962), but he made bacteriologists pause and question ideas that, by constant repetition, were becoming accepted as facts.

Anti-Adansonism or Kauffmannism. The most forceful and repetitious champion of unequal weighting of characters is Kauffmann, who in 1937 wrote: 'Salmonellabakterien sind gramnegative Bakterien, die auf Grund ihrer Antigenstruktur in das Kauffmann-White-Schema eingefügt werden können.' On this basis any Gram-negative organism sharing an antigen with a known salmonella would also be regarded as a salmonella. Since the specificity of antigens is determined by their chemical nature, the same (or closely similar) antigen may be found in more than one group defined on other characters. With this definition of the Salmonella

group, one could include in it many quite different bacteria including pasteurellas, and the group would become something quite different. Emphasis on antigenic structure has been apparent in nearly all Kauffmann's writings. He showed greater appreciation of other characters when, as chairman of the International Enterobacteriaceae Subcommittee, and perhaps influenced by the views of other workers, he wrote: 'Tribes, genera and species should be established by biochemical methods and then sub-divided serologically' (Kauffmann, 1954). Later he retracted and antigenic structure again dominated his thoughts, indicated by his statement that each serotype was to be regarded as a species (Kauffmann, 1959). His complete antipathy to biochemical characters and classifications based on them became clear when he wrote: 'The higher groups are only biochemically defined and therefore badly defined' (Kauffmann, 1963*b*). Among biochemical tests he thought that some (e.g. the organic acids; Brown, Duncan & Henry, 1924, 1926) were more important than others; of fermentation reactions he took a particularly poor view (Kauffmann, 1963*a*). Kauffmann does not limit the stressing of antigenic structure to the *Salmonella* group; he thinks that it should apply to all the Enterobacteriaceae, to the pneumococci and other organisms that are known to be divisible into sub-units on serological grounds. By his persistent advocacy of a classification based on heavily weighted characters, he is clearly the leader of those who stress the importance of one kind of character above all others. This anti-Adansonian attitude seems to deserve the name Kauffmannism.

Kauffmann is a determined advocate and because he is such an authority on salmonellas his views must be considered seriously. He spoils his case by the extremism with which he presents it, as when he says that biochemically defined groups are badly defined. He is not on firm ground even when he quotes Bruce White as an authority for equating serotypes with species. Bruce White was a man of great perception but he regarded the serotype as a stable unit and he did not conceive that what we now call transformations and transductions could occur.

Before we leave the sixth principle it is clear that we must decide for or against the Adansonian concept, but in doing so I want to refer to the subdivision of taxonomy into three sections: classification, nomenclature, and identification. This is necessary because I believe that in classification we should give equal weight to all characters, but in identification we can legitimately put different weightings on different characters. If I am Adansonian in my approach to classification there is no necessity for me to use the same approach to identification, and in fact few diagnosticians would attempt to be so unpractical in trying to identify a bacterium.

Relation of classification to nomenclature

These then, are the general principles that govern classification; they have not been codified and are likely to remain plastic and to serve more as guides than as precepts. It is perhaps unfortunate that the attempt to formulate these principles has never been made, because the development of an official code of nomenclature may suggest that naming has precedence over classification, an almost classic example of the cart being before the horse. To some bacteriologists the most important aspect of taxonomy is nomenclature, or the labelling of units. As the world's

foremost authority on bacterial nomenclature, it is not unnatural that Buchanan holds this view and he would base classification on the nomenclatural type culture; he has written that a bacterial species is 'the type culture together with such other cultures or strains of bacteria as are accepted by bacteriologists as sufficiently closely related' (Buchanan, 1955). This idealistic view (Buchananism) assumes that all bacteriologists are equally competent to pass opinions on all kinds of bacteria, and blurs the distinction between identification and classification.

PRINCIPLES OF IDENTIFICATION

The true taxonomist is a man with a mission; he often leads a cloistered life, protected from the vexations and frustrations of the everyday world, and he may well wear blinkers as opaque as any worn by a horse. He is more likely to have academic interests than to be an applied worker, a follower of Adanson rather than of Kauffmann, and an Englishman rather than an American. Living a life of seclusion, safe in his small laboratory, and surrounded by his books, his microscope (and perhaps his computer tape), he affects an unconcern for the mundane application of his work. But science has a way of making itself useful, and the useful application of classification is identification.

In the utilitarian laboratory there is probably more specialization: the individual worker concentrates on a more limited field, and may be unaware of what is going on in other, often adjacent or parallel, fields.

Identification is dependent on an earlier classification, of which it is the complement. There are three methods by which an identification can be made. (1) The method in which many tests are made before attempting to compare the unknown with known (and named) units; I have named this the *blunderbuss* method, but it would have been equally apt to call it the unthinking method. (2) The method in which the approach is *intuitive* and is often followed when we think we know what organism we shall isolate (e.g. from pus from a boil we might expect to isolate *Staphylococcus aureus*) but occasionally we are shocked into abandoning this lazy approach to identification. (3) The step-by-step or *progressive* method which uses dichotomous keys; the dichotomous keys given in *Bergey's Manual* (1957) are not altogether satisfactory, but the excellent keys drawn up by Skerman (1959) take the identification down to the generic level, those of Manclark & Pickett (1961) to species.

In *Bergey's Manual* dichotomous keys are supplemented by descriptive text, and in Manclark & Pickett's scheme by tables of characters which are much more informative. A newer progressive method uses only diagnostic tables; we first carry out a few screening tests, then consult primary diagnostic tables (Fig. 3) which lead on to secondary tables made up of more specialized tests (Cowan & Steel, 1961, 1965). In using the progressive method we put different stress on different characters; in fact a good differential test becomes an important test. The screening tests of the primary tables are all simple but important because they reveal characters of great diagnostic value. By the selection of a few important tests we can often identify the genus very quickly; for the medical bacteria the primary tables are based on less than ten characters. The more a group has been studied, the more subdivisions will have been made. It follows that the diagnostic tables of the Enterobacteriaceae,

the streptococci and the sporing bacilli are large, but those dealing with staphylococci, micrococci, and neisserias are much smaller.

I have described bacterial identification as the complement of classification; it is also its antithesis because differential weighting of characters forms an essential part, and there is a deliberate selection of features or characters for descriptive purposes. Descriptions of bacteria often leave much to be desired because the author has not been selective enough. It is surprising how few characters are needed

	a		b	
	a ₁	a ₂	b ₁	b ₂
Shape	S	S	S	S
Acid-fast	-	-	-	-
Spores	-	-	-	-
Motility	-	-	-	+
Growth in air	+	+	+	+
Catalase	+	+	-	-
Oxidase	-	-	-	-
Glucose (acid)	d	+	+	+
O-F test	O/-	F	F	F





Micrococcus		•	•	•
Staphylococcus	•		•	•
Aerococcus	•	•		•
Streptococcus	•	•	•	

Fig. 3. Part of a primary diagnostic table which, by a few characters, will identify a Gram-positive bacterium to the generic level (from Cowan & Steel, 1965).

for miniature definitions (minidefinitions) which contain the fewest possible characters to define bacterial genera (Cowan & Steel, 1965); those used must be characters that are stable and constant when looked for by different techniques. Drawing up the minidefinitions spot-lighted similarities known for some time, but ignored because their acceptance would offend the innate conservatism of taxonomists. A good example is the close similarity of *Serratia marcescens* to the motile Gram-negative rods now forming the genera *Enterobacter* and *Hafnia*, first noticed by Pederson & Breed as long ago as 1928.

The influences of media, indicators, and technical methods in establishing the characters of bacteria are now well recognized, and every effort should be made to keep the test conditions constant. Workers who devise new characterizing tests should describe their techniques in detail. Cowan & Steel (1965) adapted the nomenclatural type culture concept to cultures for characterizing tests, by designating different strains (biotest type strains) that are positive and negative in the tests used.

RULES OF NOMENCLATURE

Classification and nomenclature form two parts of taxonomy and the result of taxonomic work is conveyed to other workers by the application of labels to the microbial units. As so often happens communication is the weakest link in the taxonomic trinity, and there may be much discussion about the correctness of names given to different taxa. To try to bring order to this problem an International Committee on Bacteriological Nomenclature was formed in 1930, and a Code of Nomenclature approved in 1947 (Buchanan, St John-Brooks & Breed, 1948); this was revised and annotated by Buchanan and published (Buchanan, Cowan, Wikén & Clark, 1958). The nomenclatural Code consists of Rules and Recommendations but its weakness lies in an inability to enforce the rules, which thus become precepts of good behaviour and professional ethics. To many people the Code is unacceptable because it recognizes 1753 as the starting date for bacteriological nomenclature, and the rules are to be applied retroactively; a starting date in the era of pure cultures with automatic invalidation of many old names would be much more acceptable.

Nomenclature is only a means of labelling individual units and need not commit a worker to more than a label which must, however, be unique for each different organism. The advantages of a binomial system are twofold: (1) fewer unique names are needed than in a uninomial system; (2) relations between units can be indicated by the first (or generic) name. A disadvantage of any system of naming is that it is limited to pronounceable words; this limit has apparently been reached in epithets used for some salmonellas and in names such as *Bdellovibrio* recently proposed by Stolp & Starr (1963).

ALTERNATIVE TO NOMENCLATURE

It is possible to devise a method of labelling microbial units in which names are avoided altogether; the unique label can be a code either in the form of letters and numbers as in the telephone system, or a series of figures as in the Zip numbers used by the United States postal service. Empirical codes of this kind are not limited to pronounceable words, and figures, unlike letters in word form, can be arranged in any order as in these examples.

142148 = *Staphylococcus aureus*

142247 = *Streptococcus pyogenes*

241146 = *Escherichia coli*

241245 = *Shigella dysenteriae* 1

Six figures might not suffice to show the delicate nuances of, say, the various serotypes of *Salmonella*, but provision could be made for these finer details to be indicated after a decimal point, colon or dash.

A more elaborate descriptive code can be developed in which a few simple basic characters are given single digit numbers to form a sequential code. Of the characters used by Cowan & Steel (1961), those dealing with morphological and tinctorial features are given numbers 1 to 9 and 0; and five of these appear before the dash. Catalase, oxidase, and attack on glucose are expressed as four numbers 1 to 9 and are shown after the dash; the cipher 0 would be added for those bacteria that are

strict anaerobes. The two groups of figures are sufficient to characterize many bacteria to the generic level of an orthodox classification; more individualistic (? specific) features can be indicated by a code figure or figures after a colon. Alternatively the subgeneric unit can be shown by a purely arbitrary number (Table 1).

Table 1. *A descriptive code and examples*

Before dash	After dash
1 Gram-positive	Catalase-positive
2 Gram-negative	Catalase-negative
3 Sphere	Oxidase-positive
4 Rod shaped	Oxidase-negative
5 Acid-fast	Glucose not attacked
6 Not acid-fast	Glucose attacked by fermentation
7 Spore forming	Glucose attacked by oxidation
8 Not spore forming	Gas produced from glucose
9 Motile	Gas not produced from glucose
0 Non-motile	Does not grow in air

Number after colon = empirical number allotted to a species

13680-1469:1 = *Staphylococcus aureus*

13680-2469:1 = *Streptococcus pyogenes*

14670-1479:7 = *Bacillus anthracis*

24689-1469:1 = *Salmonella typhi*

14679-24590:1 = *Clostridium tetani*

DISCUSSION

If we are looking for a new approach to systematics in general and the classification of bacteria in particular, we must be prepared to abandon hierarchical systems which imply natural relationships, and seek new ways of building up the bigger units from the smaller subunits. First we should seek similarities of fundamental characters, and here transferable genetic material seems at the present time to be of the utmost importance. Next we may think of similarities in the cellular substance of different units; we can collect evidence from independent sources, such as chemical analysis of cell walls (Cummins & Harris, 1956; Westphal, Kauffmann, Lüderitz & Stierlin, 1960) or of antigenic structure by serological analysis. Other similarities that will help us to form our larger groups will be the metabolic activities of the smaller units; thus it is convenient to group together those bacteria that use gaseous nitrogen; in the same way those that ferment carbohydrates can be separated from those that oxidize or do not attack sugars. A build-up such as this will lead to groupings many of which are in use today, but there will not be any suggestion that the individual units making up a group are related. A classification built up in this way, utilitarian in concept, would not be hidebound by outmoded ideas on relations other than those of basic similarities. Kauffmann (1963*a*) advocated such building-up, but, in my view, his conservatism in using such terms as species, genus and so on decreases the chances of having his views accepted.

The comparison of characters is simple only as long as the known characters of the different units are few; mechanical devices help when a moderate number of characters is known (Cowan & Steel, 1960, 1961), but when many characters are to be compared a computer becomes invaluable, if not essential (Sneath, 1957*b*). The

usefulness of a computer has been shown in classification (Sneath & Cowan, 1958) and in identification (Payne, 1963), but a computer is an expensive luxury and we are now seeking ways by which it can be transferred from the cloisters of systematics to the utilitarianism of the diagnostic laboratory.

The expression of characters can be achieved better by a sequential code than by a name descriptive of some characters. Table 1 is a utilitarian system of codification rather than an elegant form of nomenclature associated for so long with classical taxonomy, but it is an example of a concept that must be given serious thought if we are to attempt to label all the permutations of characters of which bacteria are capable.

This paper is based on one read on 1 May 1964 in Washington, D.C., U.S.A. at a Symposium organized for the dedication of new laboratories for the American Type Culture Collection.

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