

plant and animal diseases. He emphasized that there is not ‘one single manner of arrangement which will be necessarily “the best” even if developed by rational minds. The relative merits of different possibilities are largely determined by the purpose to be served.’

van Niel (1946) realized that ‘our fragmentary knowledge of bacterial phylogeny is far from sufficient to construct anything like a complete system.’ So he advocated the construction of multiple keys to facilitate determinative bacteriology. Thus: ‘The development of a more satisfactory determinative system, divorced from the implications of a direct connection with a phylogenetic classification, can be initiated immediately. Our very limited knowledge of the “natural” relationships of the bacteria will not be a stumbling block for the enterprise. Meanwhile, advances in the understanding of bacterial phylogeny will depend on following such leads as may be discovered from time to time.’

Would the existence of multiple keys for determinative purposes impede the research of those working on evolutionary relationships of bacteria? Very unlikely

New names for numerous bacteria have entered the literature, largely on the basis of the ‘16S hypothesis’, namely, that evolutionary relationships can be divined simply by comparing characteristic sequences in 16S rRNA. Dissimilarity in sequences between organisms traditionally assigned to the same genus leads ‘16S disciples’ to rename organisms. This is done with little or no thought to the importance of stability of nomenclature or to practical aspects of determinative bacteriology. Such renaming could be excused if it could be demonstrated conclusively that ‘16S rRNA phylogenies’ and cellular phylogenies are identical, but this is hardly the case.

What do the following bacteria have in common? *Eubacterium barkeri*, *Syntrophospora bryantii*, *Paenibacillus durus*, *Caloramator fervidus*, *Oxalophagus oxalicus*, *Oxobacter pfennigii*, *Moorella thermoacetica*, *Thermoanaerobacter thermohydrosulfuricus* and *Filifactor villosus*. These are newly proposed names (Collins *et al.*, 1994) of previously known rod-shaped anaerobic bacteria which were once

all classified in the same genus, described generally as follows (Skerman, 1959): free-living, unicellular, non-branching, non-photosynthetic, rod-shaped organisms, anaerobic, heterotrophic, endospores are produced. The foregoing is a useful description of the genus *Clostridium*, which includes numerous organisms of importance in medical microbiology, fermentation technology, waste disposal, etc. The name changes were introduced largely on the basis of ‘16S rRNA phylogenetic trees’ which many microbiologists eagerly assumed to be equivalent to cellular phylogenetic trees.

Rampant name-changing has been propelled by the assumption that 16S rRNA sequences contain the essential information required to trace cellular evolutionary relationships. While name-changing has escalated, so have reports on the occurrence of wide-spread Horizontal Gene Transfer (HGT) among diverse types of bacteria. Because of HGT, serious questions have arisen on the validity of ‘16S RNA trees’ as representative of cellular phylogenies. Consequently, the metaphor of a simple tree branching from a single trunk is being replaced by spaghetti-like webs of intermingled branches (Doolittle, 2000). And we now see papers with titles and comments that evoke questions and doubts about the notion that the phylogenetics of bacteria have finally been solved by information encoded in 16S RNA [for examples see Gupta (2002), Doolittle (2000) and Gest & Favinger (2001)]. In a recent review of the complex genus *Pseudomonas*, Palleroni (2003) discussed the usefulness of 16S RNA sequences for some aspects of classification but concludes ‘...it has been rightly pointed out that the new rRNA phylogeny is the phylogeny of rRNA genes but not necessarily that of their hosts (Postgate, 1995), and therefore it should be used with caution in the characterization of taxonomic units.’ Premature name changing can hardly be viewed as an act of caution.

According to Gogarten *et al.* (2002), new information suggests that ‘traditional models for prokaryotic evolution based on clonality and periodic selection are inadequate to describe the process of prokaryotic evolution at the species level and that treelike phylogenies are inadequate to represent the pattern of prokaryotic evolution

Names of bacteria and their evolutionary relationships

In 1946, when little was known about bacterial genetics and many believed the genetic material consisted of protein, van Niel (1946) wrote a perceptive analysis of the history of problems in identification and classification of bacteria. He noted ‘the great significance which attaches to a stable and generally accepted nomenclature’ to eliminate duplication or multiplication of names for one and the same organism. It was clear to him that one of the important functions of classification is the need for rapid and conclusive identification of organisms, especially those of practical importance such as the causative agents of

at any level. Here we elaborate on this new understanding to show that a coherent model for prokaryotic evolution which invokes gene transfer [e.g., HGT] as its principle [sic] explanatory force is feasible and would have many benefits for understanding diversification and adaptation.'

Comments of Charlebois *et al.* (2003) emphasize the tentative nature of what currently postulated evolutionary trees mean: 'Fascinating as these conflicts are, the important point is not whether a given tree is right or wrong. Rather, we should use these trees as frameworks upon which to construct and test hypotheses about the rate and mode of microbial evolution, and to improve our analytical methods. Without conflicts, we might all be far more complacent about evolutionary theory. In microbial phylogenomics, the scientific process is alive and well!' Fair enough. In the meantime, what benefits have resulted from changes of names during the past decade?

Still another complication of the 16S hypothesis has been noted by Doolittle (2000), relating to the supposed non-transferability of 16S RNA: 'But this non-transferability is largely an untested assumption and in any case, we must now admit that any tree is at best a description of the evolutionary history of only part of an organism's genome.'

I have long regarded the 16S RNA model of cellular phylogenetics as an obvious oversimplification of the complexity of evolution in the real prokaryotic world. My view is based largely on increasing knowledge of the very remarkable intricacy of metabolism and its regulation in extant bacterial cells. The complicated networks of the metabolic machinery are awe-inspiring, and our knowledge of the metabolic map and of previously unsuspected control mechanisms continues to grow in new issues of many research journals. If there is a single type of RNA that contains the information that can explain how metabolism and its regulation evolved and was translated into diverse phenotypes affecting natural selection, it is certainly more potent than DNA. In this connection, remarks of Mayr (1998) are pertinent: 'Evolution is an affair of phenotypes. It is phenotypes, not genes, that are the objects (targets) of selection. This is now generally accepted by evolutionists after 50 years of

controversy. Indeed, the significance of a molecular change is usually best indicated by its phenotypic consequences.'

In a brief recent commentary, Lewin (2001) drew attention to a host of problems of classification that can ensue when new molecular, biochemical or other kinds of data emerge. He also noted that 'when it could be a matter of life and death, taxonomists in the medical profession do bypass molecular data that may indicate only a tiny proportion of genes distinguishing a pathogen from a harmless gut symbiont.' Lewin sees no real benefits from many proposed taxonomic rearrangements or name changes: 'They muddle our language and could introduce confusion in our libraries. Let's stick to widely accepted names and classifications whenever possible.'

Déjà vu van Niel

Young (2001) published a paper on the implications of HGT for bacterial taxonomy. No doubt he was unaware of van Niel's paper published 55 years earlier. Except for comment on a 1992 reference, Young's closing remarks could have been written by van Niel: 'The requirement that one system of classification be the basis of formal nomenclature is not supported by the International Code of Nomenclature of Bacteria (Lapage *et al.*, 1992), which is neutral in this regard; nevertheless, it appears to find support with some practitioners of bacterial systematics. An alternative view is to accept all taxonomic approaches and to recognize that there can be more than one legitimate classification, each with its implied nomenclature. In this case, the application of classification may need to be viewed more flexibly and account taken of nomenclature based on these different assumptions. For applied bacteriologists, who depend on nomenclature generated by systematics specialists, a proper caution, even scepticism, in accepting new proposals in nomenclature at face value as definitive will not be out of place. Systematists may need to give more consideration to the practical impact of nomenclatural revisions based on partial information and to avoid the dogmatism of asserting that any classification, phenetic, phylogenetic or polyphasic, is paramount, or that they offer

more than interim answers to questions of relationship.'

In summary, with all the difficulties discussed above, the taxonomists who continue a crusade of proposed name-changing owe the microbiology community answers to the questions posed... especially to our younger colleagues who may be confused when they explore the literature and encounter organism names that are unrecognizable and have no idea that many of them are bacteria that have been previously studied for decades.

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