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REVIEW ARTICLE

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Roger Yate Stanier, 1916–1982: a transcendent journey

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Abstract The Tenth International Symposium on Phototrophic Prokaryotes (Barcelona, 26–31 August 2000) was the latest in a series of conferences initiated by Roger Stanier in 1971 to create ties within the community of scientists working with cyanobacteria or green and purple bacteria. Consonant with Stanier's own work, the subjects of these conferences range broadly from systematics and ecology through genetics, biochemistry and physiology. The effort to define comprehensively the place of bacteria in the living world was the leitmotif in Stanier's work, the subject of one of his earliest papers (in 1941), and revisited for the final time in his autobiographical memoir of 1980. Salvador Luria noted that Stanier "...always pursued broad naturalistic interests along with chemical ones, deliberately emphasizing morphology and ecology side by side with biochemistry." Chronologically, Stanier's work addressed taxonomic and nutritional aspects of the cytophagas, enzyme induction and patterns of regulation of enzyme synthesis, aromatic degradative pathways, characterization of what would subsequently be called 70S bacterial ribosomes, the regulation of bacteriochlorophyll synthesis by nonsulfur purple bacteria, protection by carotenoids against photooxidative damage, the path of carbon in heterotrophy, the molecular basis of streptomycin dependence, the life cycle of *Caulobacter*, the taxonomy of pseudomonads, and, for the last 12 years of his life, wide-ranging studies of the cyanobacteria.

This paper is based on an opening lecture delivered at the Tenth International Symposium on Phototrophic Prokaryotes in Barcelona on 26 August 2000. It is dedicated to the memory of Germaine Stanier (Cohen-Bazire), who passed away peacefully at her home in Vancouver, Canada on 9 May 2001.

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"What is new and significant must always be connected with old roots, the truly vital roots that are chosen with great care from the ones that merely survive." (Béla Bartók)

Introduction

The First International Symposium on Photosynthetic Prokaryotes (ISSP) was held in Freiburg in 1973. Such gatherings have since been held every 3 years at different sites around the world and are the intellectual foci for all who work with green and purple bacteria, cyanobacteria, and prochlorophytes (Table 1). The symposia are unusual in their holistic coverage, inter alia including diversity, genomics, ecology and community structure, physiology and biochemistry, and structural biology. Roger Stanier (Fig. 1) provided the inspiration and impetus for these meetings. His intent was that: "The symposia would be held in an informal way, with no official, expensive books being published from the papers presented, the most important aim being personal contacts between participants [25]." This approach has been sustained over the years. The Tenth ISPP was held in Barcelona in 2000. On this special occasion, we followed Béla Bartók's admonition in a look back at Roger Stanier's academic lineage and at his exemplary career and contributions. This retrospective look reminds us of our dependence on his past work and offers a glimpse of the reasons why Stanier was such an inspiring research mentor to many participants in these conferences.

The 'Delft School' and the rise of general microbiology

Stanier, a student of Cornelis Bernardus van Niel (1897–1985), was a worthy lineal descendant of the Delft School of microbiology. The very history of microbiology began at Delft. Paul de Kruif's inspiring 1926 book Microbe Hunters [8] opens with the story of Antonie van Leeu-

Table 1 The International Symposia on Phototrophic Prokaryotes (ISPP)

Meeting	Year	City	Country	Game
1st	1973	Freiburg	Germany	
2nd	1976	Dundee	UK	
3rd	1979	Oxford	UK	Punting
4th	1982	Bombannes	France	Petanque
5th	1985	Grindelwald	Switzerland	Stone throwing
6th	1988	Noordwijkerhout	Netherlands	Shuffle board
7th	1991	Amherst, Mass.	USA	Basketball
8th	1994	Urbino	Italy	Dancing
9th	1997	Vienna	Austria	Bowling
10th	2000	Barcelona	Spain	Tug-of-war
11th	2003	Tokyo	Japan	

Fig. 1 Roger and Germaine Stanier at the Third International Symposium on Photosynthetic Prokaryotes (ISSP) in Oxford, UK, in 1979

wenhoek: "Two hundred and fifty years ago an obscure man named Leeuwenhoek looked for the first time into a mysterious new world peopled with a thousand different kinds of tiny beings, some ferocious and deadly, others friendly and useful, many of them more important to mankind than any continent or archipelago."

In a fascinating paper entitled "The 'Delft School' and the Rise of General Microbiology," van Niel [44] begins by describing Leeuwenhoek's work and follows with an analytic account of the Delft School and its contributions to microbiology. He notes that Leeuwenhoek (1632–1723) did not start a school: "There were no pupils who might afterwards have revealed secrets which the master had decided not to publish. But his discoveries were so spectacular and so unexpected that they could not fail to fire the imagination of others, equally imbued with curiosity, that driving force of scientific endeavor."

The second of the great Delft microbiologists, Martinus Willem Beijerinck (1851–1931), opened the doors to a rational exploration of microbial ecology by devising the enrichment culture technique, and used it in the isolation and characterization of a wide variety of bacteria. In 1898, he was the first to realize that the agent of tobacco mosaic disease represented a special, hitherto unknown class of organisms – a self-reproducing subcellular form of life – and coined the term 'virus' for such organisms. At the turn of the 20th century, Beijerinck was possibly the first to recognize that bacterial variation might reflect the occurrence of gene mutation.

Beijerinck retired in 1921 and was succeeded by Albert Jan Kluyver. Kluyver introduced the term 'comparative biochemistry' [16] and contributed greatly to delineating the 'unity of biochemistry' [17]: common aspects of metabolism in a wide diversity of organisms. Van Niel, who joined Kluyver as his first graduate student in 1922, regarded him as the third great Delft microbiologist and as the founder of the Delft School. Kluyver and van Niel used the enrichment culture technique to isolate photosynthetic and lithotrophic bacteria, and to show the amazing physiological diversity among bacteria. At the end of his A. J. Kluyver Lecture, delivered before the Society of American Bacteriologists – currently American Society for Microbiology – in May 1949 [44], van Niel did not reemphasize Kluyver's seminal contributions, rather he wrote:

"And I hope that you may be found willing to consider seriously the proposition that an important aspect of evolution consists in the acquisition of increased comprehension. Comprehension not for the sake of power – there is too much of that in the hands of too few – but for the sake of a possible evolution of man to a state in which he is no longer at war with himself and his

contemporaries, no longer at odds with nature, but an integral part of it. The implication of this is the need for recognition of the intrinsic value of the individual as the unique, potential step towards something new and better. If this is appreciated we shall also have gone far in understanding the great significance of another phase of the influence wielded by the founder of the 'Delft School.' For Albert Jan Kluyver has been a living example of this attitude towards the individual. Those who have had the good fortune of experiencing his influence can never be grateful enough.''

An elegant memorial [3] by two of van Niel's former students, Horace Barker and Robert Hungate – themselves scientists of exceptional merit – describes van Niel's work and his outstanding talents as an inspiring teacher. For 25 years, van Niel taught a laboratory course on microbiology at Hopkins Marine Station. Barker and Hungate [3] comment that: ''The list of students and auditors who attended van Niel's course between 1938 and 1962 reads like a Who's who of biological scientists in the United States, with several as well from other countries. Both directly and indirectly through his students, van Niel exerted a powerful influence on teaching and research in general microbiology for a generation.'' As a researcher, van Niel is best remembered for his discovery of multiple types of bacterial photosynthesis and for his deduction that all types of photosynthesis involve the same photochemical mechanism.

It is telling that in 1967, van Niel [45] opened his autobiographical memoir with a quote from Eric Hoffer [14]. Hoffer, who spent the first part of his life as a migratory worker and then a longshoreman, later became a widely known political and social philosopher:

''The newly emerging individual can attain some degree of stability and eventually become inured to the burdens and strains of an autonomous existence only when he is offered abundant opportunities for self-assertion or self-realization. He needs an environment in which achievement, acquisition, sheer action, or the development of his capacities and talents seems within easy reach. It is only thus that he can acquire the self-confidence and self-esteem that make an individual existence bearable or even exhilarating.''

The environment van Niel created for those who worked with him would have won the enthusiastic approval of Kluyver and of Hoffer. In an article dedicated to van Niel on his 70th birthday, Roger Stanier and Michael Doudoroff [35] wrote: ''In your laboratories, freedom reigned; and if it was sometimes a freedom that bordered on anarchy, you were willing to accept the consequence, rather than play an autocrat. Each of us was free to follow his own scientific interests, to develop his talents in his own particular way and at his own particular pace.''

Roger Stanier spent 1939–1942 as van Niel's graduate student at the Hopkins Marine Station. He described these 3 years as ''among the happiest and most productive of my life'' [33]. It is hardly coincidental that his later career was imbued with strong idealism and the drive to discover broad unifying themes in biology, characteristics shared with van Niel and Kluyver.

'The Microbial World'

The Microbial World, co-authored by Stanier, Doudoroff, and Edward Adelberg, and first published in 1957 [38], provided a rigorous framework for instruction in microbiology and remained a dominant textbook for some 30 years. Stanier's comments about The Microbial World reveal the way he thought about the place of microbiology within biology. In the preface to The Microbial World, he wrote: ''One can be a good biologist without knowing much about microorganisms, but one cannot be a good microbiologist without a fair basic knowledge of biology.'' Elsewhere he commented that the first edition of The Microbial World was published with ''a frankly propagandist purpose – that of accelerating this change (towards unification of microbiology with the rest of biology) by presenting microbiology in the framework of facts and concepts of general biology.''

Nature of the quest

A superficial inspection of Stanier's bibliography might lead one to believe that there was no rhyme or reason to the assortment of research problems that he had addressed. What was the common denominator, for instance, to studies of aromatic compound utilization by aerobic bacteria, the regulation of pigment synthesis in purple bacteria, the photoprotective roles of carotenoid pigments, the role of organic substrates in photoheterotrophy, and the mechanism of streptomycin action?

Such a belief would be grossly mistaken. Stanier sought the generalities that unite the apparent diversity of phenomena that characterize living systems. While so doing, he was also appreciative of the value and aesthetics of specific adaptations. An appropriate analogy would be to liken Stanier's research to an attempt at the reconstruction of a stained glass window of outstanding complexity and beauty by finding all of its many different pieces and determining their shapes and colors. The meaning of each of the fragments is evident only in the full reconstruction of the stained glass window. In this type of effort, every discovery, every new fact – whether derived from a biochemical study, from a taxonomic analysis, or from microbial physiology – is of interest and value as an indispensable piece of the puzzle; where the solution of the puzzle is a complete understanding of living organisms, their shared characteristics, as well as of those to which they owe their individuality.

The goal of knowing and understanding all of biology in a unified way may never be attained. But with effort and insight, one can assemble fragments of the puzzle, both interesting and important, and even glimpse

some of the broader unifying framework. In a lifetime, a single scientist is limited in the range of such achievement. But the "assembler" can make use of the findings that result from the cumulative effort of the scientific community as a whole. Stanier maintained a burning interest in the flow of new information in a broad range of disciplines bearing on biology. With his encyclopedic knowledge, he quickly separated the general from the particular, took disparate facts and wove them into coherent patterns. In his papers, he gave credit meticulously and, where appropriate, warm praise much valued by the recipients.

A comprehensive review of Stanier's research is offered in a 1980 autobiographical sketch [33], and in a 1986 memorial by Patricia Clarke [6]. The latter provides a complete bibliography of Stanier's publications. The descriptions of Stanier's research presented here only sample the wide diversity of his research.

Sequential/simultaneous induction

Many aerobic bacteria use aromatic compounds as sole sources of carbon and energy. In 1947, Stanier embarked upon an investigation of the aromatic degradation pathways in pseudomonads. Enzymology was barely out of its 'stone age' at the time. Stanier noted that "... techniques for the preparation of active, cell-free extracts were likewise lacking" [33]. These studies not only delineated degradative pathways widely distributed among different organisms, but also gave fundamental new insights into regulatory systems governing enzyme induction and the evolution of such systems.

Thus, when an inducer that was also a substrate was furnished to a bacterium, not one, but many, inducible enzymes were shown to be produced. This phenomenon occurred when the pathway for the inducer-substrate was mediated by a sequence of inducible enzymes. Whereas many catabolic pathways were biochemically identical in a wide diversity of bacterial groups, the patterns of regulation were found to be both diverse and group-specific (Fig. 2). Stanier argued that the diversity of the regulatory patterns indicated that they had evolved at a later time than the enzymes themselves.

A general protective role for carotenoids

The photosynthetic pigment system of nonsulfur purple bacteria consists of bacteriochlorophyll and one or more carotenoid pigments [27]. In 1953, Stanier embarked upon a study of the regulation of the formation of these pigments in *Rhodobacter spheroides*. This project marked the start of his wonderful lifelong collaboration with Germaine Stanier (Cohen-Bazire). In the course of these studies, Griffiths and Stanier [12] described a mutant of *R. spheroides* which accumulates only the colorless carotenoids neurosporene (C_{40}) and chloroxanthin. Aerobically, in the dark, the growth rate of the mutant was identical to that of the wild type. Exposure of photosynthetically grown cells to light and air led to rapid destruction of bacteriochlorophyll and cell death.

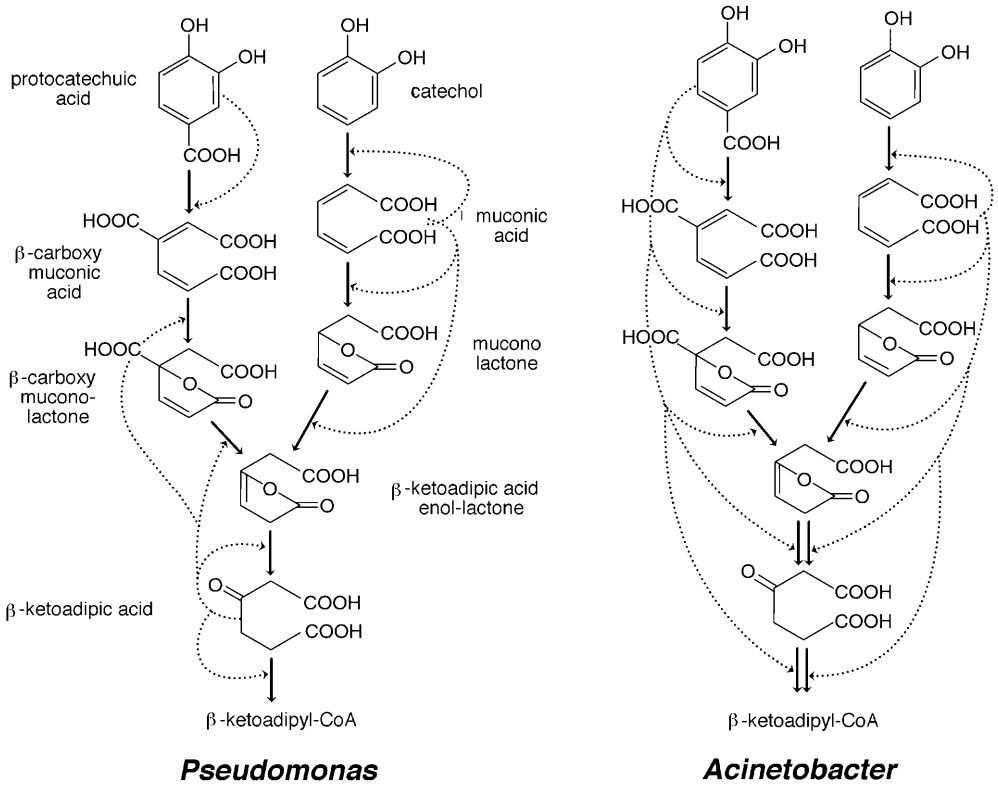

Fig. 2 Comparison of the patterns of induction in *Pseudomonas* and *Acinetoba cter* of the β-ketoadipate pathways of oxidation of protocatechuic acid and catechol. *Straight parallel arrows* indicate isofunctional enzymes. *Curved dotted-line arrows* lead from inducer to induced enzyme(s). (Modified from Fig. 12.26 in ref. [41])

The simultaneous presence of both light and air was required [28].

It was easily demonstrated that bacteriochlorophyll functioned as the photosensitizer. These studies led to the conclusion that "the carotenoid pigments associated with the photosynthetic apparatus performed an essential physiological function: protection of the cell from the deleterious effects of bacteriochlorophyll-catalyzed photooxidation" [33]. The observations in *R. spheroides* triggered an assessment of the role of carotenoids in other bacteria and in higher organisms (including humans) and led to a recognition of the general importance of the role of these compounds in vivo as scavengers of certain reactive oxygen species.

Is CO_2 fixation essential for all modes of photosynthesis?

In the mid-1950s, it was known that the light-driven reactions of photosynthesis were distinct biochemically from CO_2 fixation, a dark process. Nonetheless, CO_2 fixation was seen as essential for both oxygenic and anoxygenic photosynthesis. In 1957, Germaine Stanier found that cells of *R. spheroides* grown anaerobically in the light on acetate were filled with refractile granules and showed these inclusion bodies to be poly-β-hydroxybutyrate (PHB). Here, the ATP and reducing power generated by photosynthesis were used in the conversion of acetate to PHB rather than in the conventional pathways of CO_2 fixation. An intracellular storage material, PHB has two crucial properties: it is an osmotically inert and an essentially neutral polymer, since the carboxyl groups of the monomer, β-hydroxybutyrate, are esterified in forming the polymer.

Doudoroff and Stanier [9] soon found PHB to be widely distributed among photosynthetic and non-photosynthetic bacteria. It accumulates particularly abundantly in cells under conditions of nitrogen limitation, when a carbon source and energy are available. Stanier [33] noted that the recognition of the significance of PHB led to the clarification "of the role of primary reserve materials in assimilatory processes in general, including their role in anoxygenic photosynthesis." Many years later, Fuller and his collaborators [4,11] showed that it was possible, by manipulating growth conditions, to produce in high yield a wide variety of novel bacterial polyesters useable as biodegradable plastics with desirable properties.

The mechanism of streptomycin dependence – a retrospective look

Streptomycin can select for a class of one-step mutants in *Escherichia coli* that depend on streptomycin for growth. In 1961, Spotts and Stanier [29] correctly deduced that a misreading defect in protein synthesis in such mutants is due to a mutation in a ribosomal protein, and that this defect is "corrected" by streptomycin. In retrospect, it is evident that streptomycin dependence represents an unusual example of an allosteric effect (see ref. [7], Fig. 10–19). The prescience of the deduction is apparent considering that the 1961 publication is contemporaneous with the formulation by Jacques Monod of the general concept of allostery [43].

'The concept of a bacterium'

Ferdinand Cohn (see ref. [10]), Kluyver and van Niel [18], and Stanier [37] all made attempts to arrive at a unifying set of characteristics common to bacteria but absent from other kinds of organisms. In the preamble to their 1962 paper addressing this problem, Stanier and van Niel [37] wrote: "Any good biologist finds it intellectually distressing to devote his life to the study of a group that cannot be readily and satisfactorily defined in biological terms; and the abiding scandal of bacteriology has been the absence of a clear concept of a bacterium." They proclaimed that, finally, electron microscopy had provided the long sought set of distinctive characteristics, both negative and positive, of prokaryotic cells (those of bacteria and cyanobacteria, the erstwhile 'blue-green algae') that distinguish them from eukaryotic cells: "(i) Absence of internal membranes which separate the resting nucleus from the cytoplasm, and isolate the enzymatic machinery of photosynthesis and of respiration in specific organelles; (ii) nuclear division by fission, not by mitosis, a character possibly related to the presence of a single structure which carries all the genetic information of the cell; and (iii) the presence of a cell wall which contains a specific mucopeptide as its strengthening element" [37].

The prokaryote/eukaryote nomenclature had been proposed by Chatton [5] in 1937 to classify living organisms into two major groups: prokaryotes (bacteria) and eukaryotes (organisms with nucleated cells). Adopted by Stanier and van Niel [37], this classification was universally accepted by biologists until recently. However, in 1994, in a historical analysis of the views on microbial phylogeny, Woese [48] dubbed the period from about 1955 to 1970 "The Dark Age," and described the prokaryotic-eukaryotic dichotomy as pernicious dogma: "That midcentury shift in microbiology's world view – dismissing the search for microbial relationships, embracing the prokaryotic-eukaryotic dichotomy, and adopting the outlook and value structure of molecular biology – delayed the establishment of a phylogenetic framework for microbiology for more than a decade, causing that discipline's stunted development..." He reiterated this view in several publications, most recently in 1998 [49]: "And I believe the complacency that this simplistic formulation generated adversely affected the development of biology, for it served among other things to mask the fact that the basis for a true science of microbiology, 'the concept of a bacterium' was never developed."

Through the astute choice of the highly conserved 16S ribosomal RNA (rRNA) as a phylogenetic marker and by undertaking the task of sequencing these molecules by the laborious methods available in the 1970s, Woese made a decisive contribution to the broad understanding of the phylogeny of microorganisms [47, 50]. Phylogenetic trees based on 16S rRNA sequences revealed two distinct lineages among prokaryotes, the eubacteria and archaebacteria. The discovery of the archaebacteria and of their genetic make-up is an important piece in the puzzle of the origin(s) of the eukaryotic cell.

Are the archaebacteria (recently renamed Archea [51]) prokaryotes? The criteria used by Stanier and van Niel [33] to define a prokaryote are given above. These criteria are "equally true for the archaebacteria except that archaebacteria lack peptidoglycan [19]." It is fair to say that describing a microorganism as a prokaryote does not define its position in the tree of life. However, it does broadly characterize the cellular architecture typical of eubacteria and archaebacteria.

Trees based on small subunit rRNA sequences place the Archea closer to eukaryotes than to bacteria. However, genomic trees based on whole proteome comparisons "place the Archea in the proximity of the Bacteria when the whole gene content of each organism is considered..." [42]. The distribution of the most common protein folds is very similar in bacteria and archaea but distinct in eukaryotes [52]. Extensive lateral gene transfer among prokaryotes complicates the picture [21]. It is generally agreed that 16S rRNA sequence data are frequently not predictive of the metabolic capabilities of organisms (e.g., ref. [1]). The genomes of prokaryotic cells are mosaics of genes from a wide variety of microorganisms. It has long been recognized that the eukaryotic cell is a mosaic, and molecular data do not yet distinguish decisively between widely divergent theories as to its origin (e.g., ref. [13]). Mitochondria are derived from proteobacteria, chloroplasts from cyanobacteria [20, 22]. The eukaryotic protein synthesis machinery (transcription and translation) is closely related to that of the Archea, whereas proteins in other metabolic pathways are related to those of Bacteria. Much remains to be discovered and interpreted before we come to a convincing view of the evolutionary origin(s) of eukaryotic cells.

As for "The Dark Age," Ingraham and Nikaido [15], in a concise rebuttal of Woese's assertions, note: "Those of us who lived through the 1960s and 1970s as professional microbiologists know that this description does not reflect what actually happened. First, Roger Stanier did not destroy the enthusiasm of microbiologists for phylogeny; he stimulated it. Perhaps his principal goal throughout his professional life was to make sense of the microbial world by organizing microorganisms into phylogenetically related groups and thereby to integrate microbiology into the rest of biology." This assessment leads us to Stanier's taxonomic studies on the pseudomonads and on the cyanobacteria.

Pseudomonas taxonomy

The studies on the catabolism of aromatic compounds by members of the genus *Pseudomonas*, described under 'Sequential/simultaneous induction' above, revealed intriguing variations in regulatory mechanisms (see Fig. 2). These observations, along with the fact that "the diversity of functions found in the members of the genus as traditionally defined, served as the basis for creation of a large number of species... made imperative a revision of the systems of species classification and a search for nomenclatural accuracy" [23].

Barker [2] wrote: "In the early 1960s, Doudoroff was persuaded by his somewhat domineering colleague Roger Stanier to undertake a collaborative study of the taxonomy of the genus *Pseudomonas*." The research proceeded in two stages. The first was a laborious survey of 169 phenotypic characters of 267 *Pseudomonas* strains [39]. The characters examined were: (1) the ability to use 146 different organic compounds as a source of carbon and energy; (2) denitrifying ability; (3) H_2 chemolithotrophy; (4) accumulation of PHB; (5) nitrogen sources; (6) specific growth factor requirements; (7) the type of aerobic electron transport system (cytochrome difference spectra); (8) tests for the arginine dihydrolase system (ref. [23], p. 242); (9) biochemical pathways of aromatic ring cleavage; (10) mean DNA-base composition.

The results allowed the recognition of a relatively small number of species that differed from each other by multiple, unrelated, phenotypic characteristics [39]. After Stanier's departure from Berkeley in 1971, Palleroni, Doudoroff, and their associates examined genotypic relations among various strains by DNA-DNA hybridization and rRNA-DNA hybridization. Use of rRNA hybridization with chromosomal DNA allowed division of 35 *Pseudomonas* species and subspecies and one species of *Xanthomonas* into five distantly related groups [24]. Palleroni [23] notes that: "The competition method of nucleic acid hybridization, which had been used extensively for the DNA-DNA hybridization experiments, was adapted to rRNA-DNA hybridization studies which, in fact, represent the first example in [sic] the use of rRNA sequence similarities for the solution of taxonomic problems in bacteria." He comments also that "From the beginning, the extensive phenotypic study of *Pseudomonas* species, added to differences in biochemical properties observed in many strains under study, indicated a marked heterogeneity in the genus. The extensive amount of information helped the creation of phenotypic groups which did not differ significantly from the final scheme that emerged from the rRNA studies". In his obituary of Michael Doudoroff, Stanier [31] described the phenotypic and genotypic analysis of the genus *Pseudomonas* "as one of the great landmarks of bacterial taxonomy."

Cyanobacteria

The wide-ranging contributions of Stanier's group to the understanding of the cyanobacteria from the mid-1960s provide an indispensable foundation for much current research on cyanobacteria. The description of these studies given here is brief since they were reviewed in a number of publications by Stanier himself, which should be consulted for the original references [26, 32, 34, 40, 46]. Starting with the contributions of Mary Mennes Allen in the 1960s and continuing with the tireless efforts of Rosie Rippka and others, an enormous effort was dedicated to accumulating a very large collection of axenic cultures of diverse cyanobacterial strains. The Pasteur Culture Collection of Cyanobacteria has been, and continues to be, indispensable to progress on virtually all facets of "cyanobacteriology."

Cyanobacteria share with bacteria all of the distinctive genetic and cytoplasmic features that differentiate these two groups of organisms from eukaryotes [33]. The traditional classification of the cyanobacteria as algae ('blue-green algae') was based solely on "the resemblances between the cyanophytan cell and one constituent of the algal cell, its chloroplast" [32]. Even though Stanier and van Niel [37] asserted that: " a definition of a bacterium is only possible if one includes the blue-green algae," the acceptance of their bacterial nature was slow in coming. In Bergey's Manual of determinative bacteriology, 'Cyanobacteria' first appeared in the 8th edition in 1974. Stanier himself used the name "blue-green algae" up to the early 1970s. The first of his papers where these organisms were designated as "cyanobacteria" appeared in 1975. Stanier's efforts to change the jurisdiction over the cyanobacteria from the International Code of Botanical Nomenclature to the International Code of Nomenclature of Bacteria, started in the early 1970s and were still the subject of his (posthumous) last publication in 1983 [36]. Such a change was needed to permit replacement of existing dead type material in herbaria by living holotypes. His lack of success offers a spectacular example of the power of traditional form over substance.

In his autobiographical essay, Stanier [33] highlighted the following aspects of the research of his laboratory on cyanobacteria: (1) a partial explanation of the frequently encountered obligate autotrophy among cyanobacteria; (2) characterization of the fatty acid composition of cyanobacterial strains; (3) structural studies of phycobiliproteins and phycobilisomes; (4) the occurrence and distribution of chromatic adaptation among cyanobacteria; (5) discovery and characterization of *Gloebacter violaceus*, a unique cyanobacterium lacking thylakoids; (6) revelation of a widespread distribution of the genes encoding nitrogen fixation in nonheterocystous cyanobacteria; (7) comprehensive taxonomic studies; (8) the study of an entire order, the Pleurocapsales, on the basis of pure cultures and their patterns of growth and development.

The studies on cyanobacteria showcase Stanier's approach to biology: the desire to understand the general and the particular about the group of microorganisms of interest – their anatomy, cell biology, ecology, physiology, biochemistry, taxonomy, and evolutionary biology – and document its brilliant success.

Envoi

In a tribute to the memory of Jacques Monod, her postdoctoral mentor, Germaine Stanier [30] quoted André Lwoff "L'art du chercheur, c'est d'abord de se trouver un bon patron." Stanier met this objective, in choosing to do his doctoral work with van Niel. Like van Niel, Stanier was a mentor with admirable breadth of interests, brilliant insights, incisive analytical powers, and unshakable integrity. His most lasting legacy is in his contributions to the development as scientists of the many whom he had guided and inspired, and who now inspire new generations of young scientists.

On one occasion, Roger told me that he could think of nothing better than spending 6 months reading the collected works of Henry James. From the foregoing, it is evident that he need have no concerns about the famous dictum by William James, Henry's brother, "The great use of a life is to use it for something that outlasts it."

References

1. Achenbach LA, Coates JD (2000) Disparity between bacterial phylogeny and physiology. ASM News 66:714–715
2. Barker HA (1993) Michael Doudoroff. Biogr Mem Natl Acad Sci 62:119–41
3. Barker HA, Hungate RE (1990) Cornelis Bernardus van Niel, 1897–1985. Biogr Mem Natl Acad Sci 59:389–423
4. Brandl H, Gross RA, Lenz RW, Fuller RC (1990) Plastics from bacteria and for bacteria: poly(β-hydroxyalkanoates) as natural, biocompatible, and biodegradable polyesters. Adv Biochem Eng Biotechnol 41:77–93
5. Chatton E (1937) Titres et travaux scientifiques. Sète, Sottano
6. Clarke PH (1986) Roger Yate Stanier 1916–1982. Biogr Mem Fellows R Soc 32:543–568
7. Davis BD, Dulbecco R, Eisen HN, Ginsberg HS (1989) Microbiology, 4th edn. Lippincott, Philadelphia, p 214
8. De Kruif P (1926) Microbe hunters. Harcourt Brace, New York
9. Doudoroff M, Stanier RY (1959) Role of poly-β-hydroxybutyrate in the assimilation of organic compounds by bacteria. Nature 183:1440–1442
10. Drews G (2000) The roots of microbiology and the influence of Ferdinand Cohn on microbiology of the 19th century. FEMS Microbiol Rev 24:225–249
11. Fuller RC (1999) Forty years of microbial photosynthesis research: where it came from and what it led to. Photosynth Res 62:1–29
12. Griffiths M, Stanier RY (1956) Some mutational changes in the photosynthetic pigment system of *Rhodopseudomonas spheroides*. J Gen Microbiol 14:698–715
13. Gupta RS (1998) Protein phylogenies and signature sequences: a reappraisal of evolutionary relationships among archaebacteria, eubacteria, and eukaryotes. Microbiol Mol Biol Rev 62:1435–1491

14. Hoffer E (1963) The ordeal of change. Harper & Row, New York
15. Ingraham JL, Nikaido H (1994) The phylogeny of microorganisms. ASM News 60:293
16. Kluyver AJ (1931) The chemical activities of microorganisms. University Press, London
17. Kluyver AJ, Donker HJL (1926) Die Einheit in der Biochimie. Chem Zelle Gewebe 13:134–190
18. Kluyver AJ, Van Niel CB (1936) Prospects for a natural system of classification of bacteria. Zentralbl Bakteriol Parasitenkd Infektionskr Hyg Abt II 94:369–403
19. Mayr E (1998) Two empires or three? Proc Natl Acad Sci USA 95:9720–9723
20. Morden CW, Delwiche CF, Kuhsel M, Palmer JD (1992) Gene phylogenies and the endosymbiotic origin of plastids. BioSystems 28:75–90
21. Ochman H, Lawrence JG, Groisman EA (2000) Lateral gene transfer and the nature of bacterial innovation. Nature 405:299–304
22. Pace NR (1997) A molecular view of microbial diversity and the biosphere. Science 276:734–740
23. Palleroni NJ (1993) *Pseudomonas* classification. A new case history in the taxonomy of Gram-negative bacteria. Antonie van Leeuwenhoek 64:231–251
24. Palleroni NJ, Kunisawa R, Contopoulou R, Doudoroff M (1973) Nucleic acid homologies in the genus *Pseudomonas*. Int J Syst Bacteriol 23:333–339
25. Pfennig N (1983) Dedication. Ann Microbiol (Inst Pasteur) 134B:7–8
26. Rippka R, Deruelles J, Waterbury JB, Herdman M, Stanier RY (1979) Generic assignments, strain histories and properties of pure cultures of cyanobacteria. J Gen Microbiol 111:1–61
27. Sistrom WR (1978) Control of antenna pigment components. In: Clayton RK, Sistrom WR (eds) The photosynthetic bacteria. Plenum, New York, pp 841–848
28. Sistrom WR, Griffiths M, Stanier RY (1956) The biology of a photosynthetic bacterium which lacks colored carotenoids. J Cell Comp Physiol 48:473–516
29. Spotts CR, Stanier RY (1961) Mechanism of streptomycin action on bacteria. Nature 192:633–637
30. Stanier (Cohen-Bazire) G (1979) Remembrance of things past. In: Lwoff A, Ullmann A (eds) Origins of molecular biology: a tribute to Jacques Monod. Academic Press, New York, pp 49–53
31. Stanier RY (1975) Obituary. Michael Doudoroff, 1911–1975. ASM News 41:737–738
32. Stanier RY (1977) The position of cyanobacteria in the world of phototrophs. Carlsberg Res Commun 42:77–98
33. Stanier RY (1980) The journey, not the arrival, matters. Annu Rev Microbiol 34:1–48
34. Stanier RY, Cohen-Bazire G (1977) Phototrophic prokaryotes: the cyanobacteria. Annu Rev Microbiol 31:225–274
35. Stanier RY, Doudoroff M (1967) Professor C.B. van Niel on his 70th birthday. Arch Microbiol 59:1–3
36. Stanier RY, Rippka R (1983) A proposed system of generic designation based on studies on pure cultures of cyanobacteria. Schweiz Z Hydrol 45:273–274
37. Stanier RY, Van Niel CB (1962) The concept of a bacterium. Arch Mikrobiol 42:17–35
38. Stanier RY, Doudoroff M, Adelberg EA (1957) The microbial world. Prentice Hall, Englewood Cliffs, NJ
39. Stanier RY, Palleroni NJ, Doudoroff M (1966) The aerobic pseudomonads: a taxonomic study. J Gen Microbiol 43:159–271
40. Stanier RY, Kunisawa R, Mandel M, Cohen-Bazire G (1977) Purification and properties of unicellular blue-green algae (order Chroococcales). Bacteriol Rev 35:171–205
41. Stanier RY, Ingraham JL, Wheelis ML, Painter PR (1986) The microbial world, 5th edn. Prentice-Hall, Englewood Cliffs, NJ, p 307
42. Tekaia F, Lazcano A, Dujon B (1999) The genomic tree as revealed from whole proteome comparisons. Genome Res 9:550–557
43. Ullmann A (1979) Being around. In: Lwoff A, Ullmann A (eds) Origins of molecular biology: a tribute to Jacques Monod. Academic Press, New York, pp 165–170
44. Van Niel CB (1949) The ''Delft school'' and the rise of general microbiology. Bacteriol Rev 13:161–174
45. Van Niel CB (1967) The education of a microbiologist: some reflections. Annu Rev Microbiol 21:1–30
46. Waterbury J, Stanier RY (1978) Patterns of growth and development in pleurocapsalean cyanobacteria. Microbiol Rev 42:2–44
47. Woese CR (1987) Bacterial evolution. Microbiol Rev 51:221–271
48. Woese CR (1994) There must be a prokaryote somewhere: microbiology's search for itself. Microbiol Rev 58:1–9
49. Woese CR (1998) Default taxonomy: Ernst Mayr's view of the microbial world. Proc Natl Acad Sci USA 95:11043–11046
50. Woese CR, Fox GE (1977) Phylogenetic structure of the prokaryotic domain: the primary kingdoms. Proc Natl Acad Sci USA 74:5088–5090
51. Woese CR, Kandler O, Wheelis ML (1990) Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. Proc Natl Acad Sci USA 87:4576–4579
52. Wolf YI, Brenner SE, Bash PA, Koonin EV (1999) Distribution of protein folds in the three superkingdoms of life. Genome Res 9:17–26