

## The road from *The Microbial world* to *Microbe*

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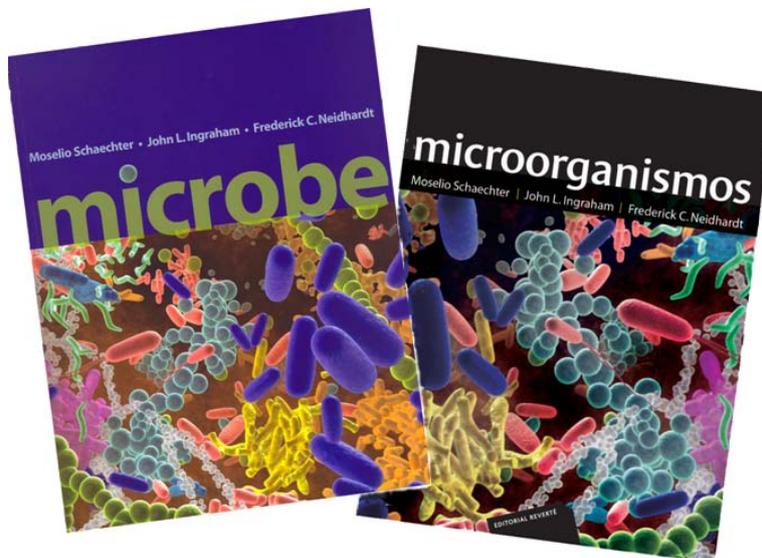
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The year 2007 commemorates the 50th anniversary of the publication of *The Microbial World*, the seminal microbiology textbook that shattered the microbiology world and whose first edition was coauthored by Roger Y. Stanier, Michael Doudoroff and Edward A. Adelberg. The year 2007 marks also twenty-five years of Stanier's passing away. The Spanish Society for Microbiology (SEM) with the support of Fundación Ramón Areces has organized a Symposium, in the frame of the 21st national congress of the SEM (Seville, 17-20 September 2007), to commemorate those anniversaries, and has invited us (Schaechter, Ingraham and Neidhardt) to contribute to this celebration.

**Writing *The Microbial World*.** One of us (Ingraham) was coauthor of *The Microbial World* from its fourth edition. In the summer of 1974 he received a life-changing letter from Stanier asking to join him and Edward Adelberg in writing the next edition of the book. He would replace, if such were possible, Michael Doudoroff, one of the original authors and a brilliant scientist, in doing the parts on physiology, biochemistry, and applications. Adelberg would continue his stewardship of

genetics, immunology, and infectious diseases. Stanier would do all the rest and, of course, he would lead, direct, oversee, synthesize, orchestrate, and criticize. Ricardo Guerrero, current SEM president and young postdoctoral fellow in Ingraham laboratory in the years 1972-1973, was paying him a visit during the summer of 1974 and surely recalls Ingraham's excitement after receiving Stanier's letter.

The three authors of the coming edition met the next summer at Ingraham's house in Davis at Stanier's insistence to put the book together. Stanier was committed to presentation almost as deeply as he was to science. The book had to sound right as well as be right. Stanier's sound test was to read the other author's offerings aloud, pausing frequently to comment and suggest rewriting. Ingraham recalls his pausing while reading something he had written



about the chemostat, horrified that Ingraham had called it a device. "Device sounds so sinister." Marjorie—Ingraham's wife—fed them, typed the complete manuscript with three carbon copies, and proofread it. She also sewed the cuffs on Roger's new trousers. She had the toughest job and busiest summer of all.

At Stanier's request, Ingraham went on to lead the writing of the fifth edition without Stanier's help, as by then he became quite ill, but with the valuable participation of Mark L. Wheelis and Page R. Painter. The publishers, of course, were anxious to do subsequent editions, but somehow it never seemed quite right to Ingraham, who found himself (during the preparation of the fifth edition) attempting to write with Roger's voice and hearing him read it aloud. He decided that the book should appropriately end with Roger.

Stanier was a remarkably productive microbiologist. Certainly, his essay on what is a bacterium, and studies on metabolism of aromatic compounds, taxonomy of pseudomonads and cyanobacteria are monuments of modern microbiology. But his proudest achievement, as he said, was writing *The Microbial World*. He mentioned that often in his final days. He always said that his purpose for writing it was to make microbiology a part of biology from which it had always been curiously isolated. The book certainly was a force in that movement, now accomplished—so fully accomplished that it is difficult to imagine that it was not always so.

Stanier's major aim in science was to present microbiology as a logical, coherent science and *The Microbial World* was one of his major vehicles. His classic 1962 paper with C.B. van Niel, "The concept of a bacterium" [4] reveals that passion, as do his intense investigations on taxonomy of *Pseudomonas* and cyanobacteria. Of course, things changed since those studies—the archaea were discovered, as were powerful new molecular methods to deduce microbial phylogeny. Roger would have embraced them fully as he did earlier molecular methods such as DNA hybridization. Inexplicably, some have concluded that Roger's early attempts at finding structure and coherence in microbiology, probably because they were clearly and convincingly presented, were an impediment to the science's progress [2]. Of course, crisply defining questions and clearly stating positions are always stimulants, never an impediment. This Symposium shows that many of us continue to value Stanier's clarifying contributions to microbiology.

**Origins of Growth of the Bacterial Cell and Physiology of the Microbial Cell.** One of us (Neidhardt) was a graduate student at mid-twentieth century, and was pleased and relieved when he opened a textbook that finally showed him how his interest in bacterial growth fitted into the larger scheme of the biological world. As another of us (Ingraham) has said, *The Microbial World* clarified the notion of a bacterium, and placed microbial studies firmly within the framework of biological thought, providing a structure that served microbiologists and biology students

well in assimilating the additions, corrections and amendments provided by later molecular studies.

*The Microbial World* opened a trail that has led to the current introductory text *Microbe*, through two advanced books on bacterial physiology. Two of us (Ingraham and Neidhardt) along with Ole Maaløe worked on one of these books in the early 1980s trying to summarize our thinking about the process of bacterial growth, our conception of the subject that was molded by what we had learned from *The Microbial World*. The product was *Growth of the Bacterial Cell* (Sinauer Associates, Sunderland, MA, 1983). Our decision to focus on growth as a preeminent property of bacteria (and a central property of all living systems), was easily made, for it grew out of studies that had engaged the three authors for many years, in Davis, Copenhagen, Paris, West Lafayette, and Ann Arbor.

Three features of *Growth of the Bacterial Cell* distinguished it from any other treatise on bacteria. One was the attention it placed on the need, in quantitative bacterial growth studies, to establish reference conditions and to achieve balanced growth, recognizing that these were essential for reproducibility of bacterial cultures. This subject was given prominence by placing it as the book's opening argument. Today its message is heeded by a new generation of students, who are coming recently into bacterial growth studies from physics, engineering, and systems modeling.

Organizing metabolism into an all-embracing framework was a second feature—one that has become widely adopted. Every metabolic reaction was placed into one of four domains: fueling, biosynthesis, macromolecule synthesis, and assembly. From estimates of the composition of an *Escherichia coli* cell at a particular rate of balanced growth, the total consumption of carbon, ammonium, phosphate, ATP and reducing equivalents was calculated and tabulated for each of the metabolic domains. This treatment of metabolism, with its material and energetic balances required for growth, and its concept of the 13 precursor metabolites, had been the inspiration of H. Edwin Umbarger, a giant in the field of 20th century bacterial biochemistry.

The third unique feature of *Growth of the Bacterial Cell* was the introduction of the concept of growth rate as a variable in growth physiology. The chapter bearing this title ("Growth rate as a variable") dealt with the striking extent to which one can, for a given temperature, predict the chemical composition of the bacteria cell from its steady state growth rate. This concept still disturbs many investigators, who object to calling the growth rate a "variable" rather than a dependent consequence of the nutritive richness of the medium. In fact, the beauty of the concept lies in the vision that the composition of the cell in any given medium is the cell's

steady state solution to the integrative nutritive value of the medium, and to a first approximation is independent of the precise chemical nature of the medium. It has been a close family. The same woman, Marjorie Ingraham (1923-2005), who mended Roger Stanier's trousers 1975, also provided support for Neidhardt's wife, Germaine, and infant son Marc Chipault, as work progressed on *Growth of the Bacterial Cell* at her home in Davis seven years later.

The novel elements of *Growth of the Bacterial Cell* were continued in its sequel *Physiology of the Microbial Cell; a Molecular Approach* (Sinauer Associates, Sunderland, MA, 1990) written by the three of us. It will come as no surprise to find that these elements have found their way into our new textbook, *Microbe* (American Society for Microbiology Press, Washington, D.C., 2006).

**The phylogeny of *Microbe*.** The three of us have written or edited microbiology textbooks at several academic levels. In the United States and in some other countries, didactic courses in microbiology are offered at various stages in the academic process. The most basic level is aimed at first- and second-year university students of allied medical professions, such as nursing, nutrition, and physical therapy. These students are not expected to have a thorough background in biology and chemistry. The next level is for third and fourth year students who consider biology, in some form, their principal field of study. These students are expected to be somewhat proficient in biochemistry, genetics, and molecular biology. Finally, medical, dental, and veterinary students take specialized courses of importance to their profession. We are aware that those who spent time in North American universities are acquainted with this system, but others may be less familiar with it.

The textbook *Microbe* is intended for the second of these levels. Its origin stems from our teaching experience for these students. We agreed that the previously existing textbooks, although well written and illustrated, did not quite achieve what we wanted in such a textbook. Most of them are intended to be quite complete, serving as reference books, and the most representative of that genre are excellent for their purpose and we greatly admire them. However, in our view they did not resemble the textbooks of old. Those were relatively thin books designed for actual studying rather than for consultation. We therefore endeavored to return to the older concept and to write a modern version of such a book. Our direct forerunner was in fact the first edition of *The Microbial World*, a book that in its time fulfilled the same purpose and did it to near perfection.

We approached writing this book with the classroom in mind. We limited the coverage of material to only a little

more than what can be reasonably covered in lectures. The result is that our book is about half the size of others (and weighs less than half as much). In addition, trying to provide students with a book they could actually read, we strove for a discursive style, explaining to the reader why we thought that a given topic was interesting and how it fits in a general scheme. We have been told that we succeeded, at least in part. However, students who mainly like to look up facts, especially for the purpose of memorizing them, may find this book inadequate.

We should share with you some details of our interactions. We have written or edited together five books. It is fair to say that by now we know each other's way of thinking and, not infrequently, can finish another's sentence. We disagreed very infrequently and when we did, we asked: "Who cares the most about this issue?" Whoever did, won. We do not recommend this procedure for settling national issues of war and peace, but it worked well on our diminutive scale of activities.

Yet another philosophical basis steered our efforts. In the past, our writing had been greatly facilitated by the impetus from general guidelines, which are conceptual frameworks or scaffolds on which information could be placed in a logical way. Here, we adopted as a guiding principle to make the connection between what microbes do and what they look like, and the relevance of these facts in space and time. In other words, ecology and evolution. We appropriated Dobzhansky's famous dictum that "nothing in biology makes sense except in the light of evolution," and extended it to include ecology. Of course, not everything that is important about microbes can be explained that way but even if it can not, it is worth asking the question.

Under the tutelage of such principles, we extended our interests from laboratory based microbiology to the wide world in which microbes exist. We should say that other books have done the same thing and that modern microbiological textbooks are, generally speaking, ecologically-minded. This is an absolute necessity because our field is undergoing the third of its true Golden Ages [1,3]. In brief, the first Golden Age was the origin of our science, the discovery of microbes as disease agents and their role in the environment. This magnificent era was followed some 60 years later by the second Golden Age, the emergence of molecular biology and its firm basis in microbial model systems. Currently we are living in the third such age. All of biology is undergoing a phenomenal revolution due to genomic, imaging, and other methodological breakthroughs. But what distinguishes microbiology is the realization that microbes play a far more important role on Earth than had previously understood. They not only make up perhaps half the total biomass, but

they participate in key ways in the metabolism of this planet, the state of health and disease of all its occupants, and hold hope for the future of food and energy sources. There is no conceivable end to the importance of microbes, now and in years to come. Our political leaders all need a course in microbiology!

We are very pleased that this small aspect of microbiological history is being recognized at the 21st national congress of the SEM, and that this meeting has provided another occasion for us to enjoy in person our half-century of friendship.

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### About the authors

**Moselio Schaechter** was born in Italy, lived in Ecuador as a teen, and obtained his Ph.D. at the University of Pennsylvania. He spent most of his academic life at Tufts University School of Medicine and moved to San Diego in 1995. His research interests involved aspects of bacterial physiology, including growth rate regulation, membrane biology, and chromosome transactions. He served as president of the American Society for Microbiology in 1985-1986. (mschaech@sunstroke.sdsu.edu)

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