

Thomas D. Brock

Annu. Rev. Microbiol. 1995. 49:1–28 Copyright © 1995 by Annual Reviews Inc. All rights reserved

THE ROAD TO YELLOWSTONE—AND BEYOND

Thomas D. Brock

1227 Dartmouth Road, Madison, Wisconsin 53705-2213

KEY WORDS: microbial ecology, thermophiles, biotechnology, history, limnology

CONTENTS

Introduction								
Beginnings								
First Professional Work								
First Academic Appointment								
Indiana University								
Steps Toward Microbial Ecology								
Friday Harbor Laboratories								
From Leucothrix To Yellowstone								
Discovery of Thermus aquaticus								
Bacteria in Boiling Water								
"Life at High Temperatures": the Scie	ence I	Paner						
Travels in Search of Hot Springs		uper	• • • • •	•••••			• • • •	• • • • •
Deep Sea Vents								
Microbial Prospecting in Yellowstone	••••	• • • • •	••••					• • • • •
Biology of Microorganisms	••••	• • • • •	••••	•••••	••••			
Beyond Yellowstone					• • • • •		• • • •	
History of Microbiology								
Computers								
Publishing								
Final Words	••••		••••			• • • •	• • • •	• • • • •
	• • • •	· · · · ·	••••	•••••	••••	• • • •	• • • •	• • • • •

Abstract

This memoir describes the professional life and times of Thomas D. Brock, with an emphasis on those aspects of his career relating to research in microbial ecology, and how this work led to field research in Yellowstone. The first discovery of extremely thermophilic bacteria is described, followed by a discussion of some of the consequences of this discovery for biotechnology and

microbiology. Also covered briefly in this memoir are Brock's activities in textbook writing, publishing, computers, and the history of science.

Introduction

The trajectory of my career provides an example of what can be done with a little knowledge, a fair bit of luck, and a lot of hard work. It also does not hurt to have had a good set of parents.

As I had only two microbiology courses during my university studies, one of which was a so-called nonmajors course, I am mostly a self-taught microbiologist. In fact, I am self-taught in almost everything. Yet the education I did receive laid the intellectual foundation for what I have learned.

I started out in botany, then specialized in mycology and yeast physiology, and after my PhD I worked in antibiotics research in the pharmaceutical industry, a move that brought me into microbiology and molecular biology. After leaving industry, I developed a brief, albeit successful, career in yeast genetics before becoming a medical microbiologist specializing on the streptococci. In 1963, I began work in marine microbiology, which brought me into microbial ecology. For seven or eight years I juggled research on antibiotics, yeast genetics, streptococci, and marine microbiology, before finally concentrating on microbial ecology with an emphasis on extreme environments. This work led me into geology and biogeochemistry. Later I became a specialist on lakes and limnology, before closing out my scholarly career in the history of science. Throughout most of my professional life I have also had a parallel career as a textbook author. Because of this, I taught myself how to use computers and became a pioneer in the use of microcomputers in scholarly work. This path led me into publishing and editing, and I established and ran my own publishing company.

I am a member of a favored generation, finishing high school in 1944. Too young to be killed in World War II, I was able to ride to the top in the post-war prosperity of the United States. My professional life encompassed the post-Sputnik years in the United States, when money for research was easy to obtain.

Although this is a memoir, it is not based just on memory, but on extensive documentation. For better or worse, I have been a "saver," and through the vagaries of life I have managed to keep my files more or less intact. I have gone through these files in detail in preparation for writing this article in order to keep my facts straight.

1

Beginnings

I was the only child of Helen Sophia Ringwald, of Chillicothe, Ohio, and Thomas Carter Brock, of Toronto, Canada. I was born (September 10, 1926) and raised in Cleveland, Ohio, and although I have traveled extensively, I have made my permanent residence in the midwestern states all my life. Cleveland is predominantly an industrial city, but our house was on the top of a hill in a unique cul-de-sac adjacent to an errant farm and a forested park. There was a distant view of Lake Erie from the front porch. Although a short walk down a quite steep hill brought us to one of Cleveland's major thoroughfares (Euclid Avenue), behind our house were fields, cows, woods, and open spaces.

I grew up during the depths of the financial depression of the 1930s. My father had only an eighth-grade education but continued to educate himself through correspondence courses and self-study. Eventually, he became a power engineer, working in various industries in Cleveland. Although we were never well-off, my father did have a job throughout the depression (in the boiler room of St. Luke's Hospital) and my mother (who had been a registered nurse) was able to remain at home. In this working-class household, we had no music, no literature or art, and very few books. But I did have a stable home life in a pleasant neighborhood with lots of friendly playmates. In those days the schools in Cleveland were good and it was through them that I was introduced to music (the Cleveland Orchestra) and art (the Cleveland Institute of Art).

Unfortunately, when I was almost 15 my father got sick and we had to leave this idyllic environment and move to my mother's hometown, Chillicothe, Ohio. Within months my father was dead, and my mother and I lived through my high school years in what could best be called gentile poverty. I had to help financially and worked at a variety of clerical jobs in drug, clothing, and grocery stores. Because of the war-time labor shortages, I had no trouble finding work, but the pay was low (\$0.25 per hour).

My father had always recognized his lack of formal education and encouraged me to think about college. He brought home discarded electrical equipment and showed me how to make coils, electromagnets, and radios. When I was 10 years old, I received a chemistry set for Christmas and he helped me set up a simple laboratory in the basement. After we moved to Chillicothe, I met David Thornburgh, who was also interested in chemistry, and he and I set up a small research laboratory in the loft of a barn behind my house. We did lots of crazy experiments (explosives, toxic gas), but Thornburgh had also heard about penicillin (this was 1943), and we made some fleeting attempts to enrich soil for antibiotic-producing microorganisms. Hence, I decided to go to college and become a chemist.

However, the war was on, so after graduation from high school I enlisted in an electronics program in the US Navy, spending about 18 months in various Navy schools in the Chicago area. I finished out my Navy career in Kodiak, Alaska, where I worked not in electronics but as a member of the Shore Patrol. One of my jobs in the town of Kodiak was to clear the bars of sailors at curfew and to make sure the brothels were empty. After my sheltered home life, the Navy was a riotous experience. Although I had always been a reader, I had never had any contact with great literature. However, in the Navy I began to read voraciously. Soon I had decided to become a writer.

As a military veteran I was eligible for the GI Bill, and in the fall of 1946, I enrolled at Ohio State University. Although I was a good student at OSU, I soon began to have doubts about a writing career and began to think again about chemistry and science. One reason may have been Sinclair Lewis's *Arrowsmith* (the protagonist of which was a research bacteriologist), a book I was required to read in a twentieth-century American literature course. However, for reasons too complex to go into, I did not major in bacteriology but in botany, graduating (with honors) in 1949.

I was offered a graduate assistantship in botany at OSU, and with my limited financial resources, I found it difficult to go to another school. However, the study of higher plants soon bored me and I switched to mycology, receiving my MS and PhD working on a mushroom (*Morchella esculenta*) and the yeast *Hansenula anomala* (3, 5).

Although I learned very little bacteriology as a student, I did learn a lot about plant ecology. The ecology group at OSU was very strong, and I had the pleasure of taking courses from John N Wolfe, an enthusiastic lecturer. Wolfe was above all a field-oriented ecologist, and every Saturday he took us on a field trip to an interesting habitat. Furthermore, a lot of my fellow graduate students were plant ecologists. One friend, Theodore Sudia, coaxed me to think about microbial ecology. Although years would pass before I would finally move in this direction, Sudia's sharp discussions along these lines stuck with me.

First Professional Work

I received my PhD in 1952. I had been hoping for a faculty position, but at this time academic jobs were very hard to find, and postdoctoral positions were virtually nonexistent. I obtained for the summer a position as a temporary research associate working on soil fungi at the Ohio Agricultural Experiment Station (Wooster, Ohio) and spent most of my spare moments looking for a job. Fortunately, a position in the Antibiotics Research Department at The Upjohn Company came along, and because of my work in soil mycology, I was offered the job. I abandoned hope of a teaching position and went off with my new wife, Louise, to Kalamazoo, Michigan.

I actually became a bacteriologist via on-the-job training during my Upjohn years, learning from my Upjohn colleagues, most of whom had received their degrees from midwestern bacteriology departments. Antibiotics research is microbial physiology under the simplest possible conditions, and it was quite easy to pick up. By the time I left Upjohn five years later, I had published papers in respectable journals (6), had become a member of the Society of American Bacteriologists, and had attended the society's annual meetings in New York, Houston, and Detroit.

Two other accomplishments came out of my five years in Kalamazoo—an interest in historical research and a knowledge of German. Because industrial research was an eight-to-five job, I had lots of free time. Interest in an abandoned railroad near my home led me to begin doing research in local history. I had soon published a lengthy article on my railroad research in a scholarly journal (4). In my last two years in Kalamazoo, I also began studying German, using records and audio tapes. Although I never quite reached fluency, I did become adept at translating scientific papers, a skill I was eventually to use extensively in my work on the history of microbiology.

First Academic Appointment

I left Upjohn because I became bored with the routine research program and the lack of control I had over my own work. Being out of the academic world, I had quite a bit of difficulty finding an academic job, but I finally managed to obtain one in my old hometown, Cleveland, in the Biology Department of Western Reserve University (WRU, now Case Western Reserve University). It was a rather poor department; the teaching load was enormous; and the salary was miserable (about half my Upjohn salary), but it gave me the opportunity to develop my own research program and to teach microbiology rather than botany. Another attraction was that across the street in the medical school was a very fine Department of Microbiology, where I could attend seminars and borrow equipment for my research.

At WRU I taught general bacteriology to the undergraduates, and two separate courses in nursing microbiology, one for degree students in the School of Nursing, the other for nondegree students from three hospitals in Cleveland. In addition to giving all the lectures, I had to supervise the laboratories, unfortunately without any qualified teaching assistants. In subsequent semesters, I taught mycology, medical microbiology, and an advanced microbiology course that was predominantly microbial physiology and genetics.

Although I had learned a lot of microbiology at Upjohn, it was rather narrowly focused. Teaching is the best way to learn, and after two years with this heavy teaching load I was well on the way to becoming a real microbiologist. Surprisingly, I also found time for some significant research. I obtained two research grants, one from the NIH on the mode of action of antibiotics and one from the NSF on yeast mating. I had never used radioisotopes as tracers, but I ordered some and taught myself how to work with them. (In those days, one could order 50 μ Ci of any ¹⁴C compound without a license!) Louise worked as a technician and collaborator on the NIH grant, but I did the yeast work myself. By the time I left the Biology Department, Louise and I had done enough research to publish 13 papers (for instance, 7, 9, 30).

I also continued my study of German, and during the summer of 1958 I did most of the translations for what would become my first book, *Milestones in Microbiology* (8). Doing *Milestones* combined two areas that had been hobbies during my Kalamazoo days, German and history. The book was finished just before I left Cleveland and initiated a long-term relationship with the publishing company Prentice-Hall that has continued to this day. However, after *Milestones* many years passed before I returned to serious work on the history of microbiology.

Now that I was out of industry I had more free time for vacations. Louise's father was member of a wilderness fishing camp on Lake Memesagemissing in northern Ontario, and I also joined, spending the months of August in 1958 and 1959 in veritable isolation. I brought along my *Milestones* project to work on, but mainly I learned about boating and fishing, which introduced me to the aquatic environment and got me interested in canoeing, kayaking, and the great outdoors. I had never really done things like this before, and these years were to provide important background for my later research in marine microbiology, limnology, and microbial ecology.

After the second year of teaching nurses and general bacteriology, I realized that the teaching load in the Biology Department at WRU was so heavy that I would never be able to develop a really significant research program. Then LO Krampitz, Chairman of the Department of Microbiology, offered me a postdoctoral position. I resigned my Assistant Professor position and moved across the street. The research project I was assigned, on the biosynthesis of the M protein of group A streptococci, turned out to be a dead end, but it taught me a lot of biochemistry, as well as a fair bit of immunology and clinical microbiology. Krampitz's department was packed with top-flight people, many of whom went on to distinguished positions elsewhere.

Before beginning my postdoctorate, I had taken the bacterial genetics course at Cold Spring Harbor, where I associated with many distinguished geneticists and molecular biologists. As usual, I learned as much from my fellow students as from the faculty. (Many of the students would become distinguished scientists: Julius Adler, Marshall Nirenberg, Gordon Tompkins, David C White, Solomon Bartnicki-Garcia.) Many years later I returned to Cold Spring Harbor when I wrote my book on the history of bacterial genetics (27).

During the year I was in Krampitz's laboratory, I continued to supervise the research that Louise was still conducting in the Biology Department for my NIH grant. Also, because they had been unable to find a replacement, I still taught the undergraduate bacteriology course. Although this was a traumatic year in many ways, at long last I was in a legitimate microbiology department and associating with real microbiologists. By the time I left WRU I could talk bacteriology without making a fool of myself.

Indiana University

As chance would have it, toward the end of my first year as a postdoctorate, a position opened up at Indiana University (IU) in Bloomington. By this time, I had had enough of a large industrial city, even if it had been my hometown, and the small university town of Bloomington seemed quite attractive. The chairman of the department, LS McClung, offered me a position as an Assistant Professor of Bacteriology, which I accepted enthusiastically, even though the teaching responsibility was medical microbiology. Joining the IU department made my shift from botany to microbiology complete.

Although I had received my PhD in 1952, it was just now, eight years later, that I finally could get down to long-term work. In a way, it was fortunate that I had waited to settle in, since the 1960s were a time when the US economy was flourishing. Also, it was a time of greatuniversity expansion, with a special focus on increasing research activity. Training grants were easy to come by, and most of my early students at IU were supported by a Microbiology Training Grant (NIH), which allowed me to reserve my own grants for the salaries of technicians. Because of the baby boomers, enrollment was increasing. Everyone was in an expansionist mood. It was quite easy to obtain money, support, students, space, etc. Also, prices were relatively low.

However, the position at Indiana University required that I teach and do research in the field of medical microbiology. I had taught a few medical students at WRU, and a lot of nurses, so I had a fair grasp of how to put such a program together. Based on my postdoctorate work at WRU, I obtained two grants on streptococci, one of which involved extensive work on genetics and phage. I also did a lot of work on amino acid and peptide transport in enterococci (38) and finished up the work on the mode of action of antibiotics that I had begun at Upjohn and continued at WRU. With several students and technicians, I became heavily involved in research on streptococcal genetics. Probably because of my medical emphasis, I had no difficulty obtaining one of the newly established Research Career Development Awards (RCDA) from the NIH. Nepotism rules prevented Louise from working in my laboratory (later she was permitted to work as an unpaid research associate), but I had no difficulty finding competent students (34, 49) and technicians (for instance, 36, 37).

Steps Toward Microbial Ecology

During my three years at WRU, my interests in ecology had been strongly suppressed. However, I continued to think about microbial ecology, and with the RCDA to pay my salary (and a consequent reduction in teaching load), I decided that now was the time to take some steps in this direction. I had always been interested in aquatic and marine microbiology. When I took the bacterial genetics course at Cold Spring Harbor in the summer of 1959, I had lived within view of Long Island Sound and had been fascinated by the marine life and changing tides. Canoeing and kayaking in Ontario and Florida also furthered my interest in freshwater habitats.

I once read that play in children is never just play, but the first steps toward building useful skills. Outdoor activities such as canoeing and backpacking certainly fit into this category for me, as once I became involved in microbial ecology research, I not only used the outdoor skills I had acquired, but I also used the equipment I had bought. One reason I became so firmly field-oriented in my research may have been because I had become so enamored of the outdoors.

In November 1962, just before attending the American Society for Cell Biology meeting in San Francisco, I visited the laboratory of CB van Niel at the Hopkins Marine Station, Pacific Grove, California. This was the first time I had ever been at a marine station, and although this was hardly a typical marine laboratory, I found the environment quite fascinating. I had always been a fan of John Steinbeck's books and was excited to see the area around Cannery Row.

Friday Harbor Laboratories

A major turning point in my career came in the spring of 1963 when I made plans to actually do research at a marine laboratory, Friday Harbor Laboratories of the University of Washington. I had learned about this laboratory from Brooks Church, a seminar visitor at Indiana who was at that time on the faculty at the University of Washington. Through Church, I made contact with the director of the laboratory and applied for research space for the summer of 1963. The research I proposed, on the presence of enterococci in marine animals, was excessively naive, but it was a logical progression from my streptococcus work. I arrived at Friday Harbor about July 1 and stayed through the middle of August. It was a complete change of pace from Indiana, not only because of the marine environment and the quaint laboratories, but because of the chance to associate with field-oriented biologists in a variety of disciplines. I had always had broad interests; Friday Harbor showed me how these interests could be channeled in new ways.

However, my work on streptococci in marine animals lasted not much more than two weeks. Through a circuitous but logical route, I moved from ostensibly marine streptococci to *Leucothrix mucor*, which I discovered to be a widespread marine microorganism. I taught myself how to isolate pure cultures directly from nature, instead of using the accepted but unecological enrichment culture technique. The resulting work could best be called autoecological. My first paper on knots in *L. mucor* made the cover of *Science* (11) (Figure 1) and was featured in the New York *Times* (May 15, 1964). My work on *Leucothrix*

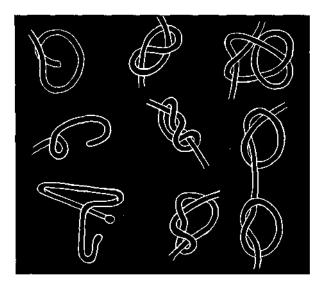


Figure 1 My first paper on knots in L. mucor made the cover of Science and was a feature article in the New York Times. Reprinted from Science, copyright © 1964 (11).

extended over the next eight or nine years and resulted in quite a few papers and two PhD theses (1, 16, 17, 41).

My L. mucor work is beyond the scope of the present article, but it is important to note that it not only pushed me toward research in general microbiology, but got me interested in sulfur springs, the habitat of members of the related genus *Thiothrix*. From cold sulfur springs I quickly moved to Yellowstone hot springs.

In addition, the Friday Harbor work led me to begin writing *Principles of Microbial Ecology* (14), which really focused my mind on what microbial ecology was all about. I began making contact with limnologists and macroecologists and understood that the proper approach to microbial ecology was through direct studies in the natural environment. My training in plant ecology at OSU certainly had a lot to do with my insistence on studying microorganisms directly in nature. Thus, even though my principal research continued in the areas of streptococcal genetics (10), yeast mating (I had just obtained a new NSF grant in this area) (12, 13, 39), and the mode of action of antibiotics [which led to the first of three invitations to the Society for General Microbiology annual symposium (15)], my reading over the period 1963–1964 concentrated on microbial ecology, as I worked on the first draft of my microbial ecology book (14).

From Leucothrix to Yellowstone

Although I had become interested in sulfur springs because of *Thiothrix*, hot springs were another matter. I had never seen any, nor had I any desire to go to Yellowstone because of its reputation as a heavily visited "amusement" park, rather than a natural area. My first visit to Yellowstone, on the way to Friday Harbor in July 1964 after a backpacking trip in Grand Teton National Park, was a revelation. I had not expected such enormous developments of microorganisms as were present in the runoff channels of the Yellowstone hot springs. Returning from Friday Harbor that summer, I stopped again in Yellowstone, and this time I sampled some hot springs, looking for possible habitats for *Thiothrix* (Figure 2).

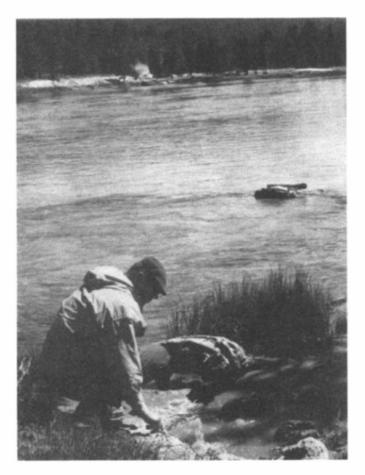


Figure 2 Sampling a small hot spring along the Yellowstone River, August 22, 1964.

Soon after returning to Bloomington, my interests in the Yellowstone habitats broadened as a result of further work on my book. By this time, I was reading a lot of the ecosystem literature, with its focus on steady-state systems. I began to think of springs as steady-state ecosystems (19).

However, I did my first work in Yellowstone to get some field experience before research planned for the summer of 1965 on the new volcanic island of Surtsey, which had developed off the south coast of Iceland (28). Thus, Louise and I visited Yellowstone again in late June and early July 1965. We planned this trip, which was one of the more exciting two weeks of my career (even though it rained most of the time), as a working vacation. The focus was to be on the thermal algae (cyanobacteria, actually) that formed the colorful mats found in the outflow channels of many of the springs and geysers.

Casual observations the previous summer had indicated that the outflow channels of Yellowstone hot springs often had extensive developments of photosynthetic organisms. I reasoned that if these effluents were steady-state ecosystems, quantitative measurements of chlorophyll in the thermal gradients should be possible. However, as an additional twist, I planned to measure not only chlorophyll, but also macromolecules: RNA, DNA, and protein. Therefore, we gathered supplies and equipment that could be taken along for such assays (Figure 3).

While getting ready for the Yellowstone trip, I had decided that I should set up some culture studies to attempt to get growth of high-temperature bacteria. Thus, I came to Yellowstone in June 1965 with supplies of bacterial nutrient media, and I tried to obtain growth at high temperatures using hot spring water as the inoculum, and the springs themselves as incubators.

Although these culture experiments came to naught, they did lead to an important discovery. In the outflow channel of a spring in the White Creek area, which we called Pool A (Octopus Spring), I saw pink gelatinous masses of material, obviously biological, at surprisingly high temperatures. The notes on this, from page 62 of field book L-IV for June 20, 1965, read in part as follows: "Pool A. N.E. of The Diamond. White Creek drainage.... Effluent at 82°C has pink gelatinous stringy (organism?). In strong flow.... Micr. exam of pinkish material. Long thin *Vitreoscilla*-like filaments, wavy, attached more or less to a central core of similar fils. Very heavy growth. Definitely living...." [*Vitreoscilla* was a gliding organism that I had made some observations on at Friday Harbor.]

Using the assays we had worked out, we found that although the pink material had considerable protein, there was no chlorophyll, although chlorophyll could readily be found in samples from temperatures below 70°C. I became convinced that the pink material was definitely bacterial and that bacteria, but not phototrophs, were living at temperatures near boiling (see

also below). These observations led me to commit early to the idea of what I later called extreme thermophiles (hyperthermophiles).

The state of research on thermophilic bacteria at that time is exemplified by the following quote: "By incubating enrichment media at very high temperatures (e.g. 55 or 60°C), cultures of thermophilic bacteria can be obtained" (47). Note what was meant here by high temperature. I have never been fond of the enrichment culture technique for research in microbial ecology, and this quotation provides one reason why. The study of microbes directly in the natural habitat led to the discovery of extreme thermophiles. A reliance on enrichment culture techniques and standard incubation temperatures of 55°C had caused investigators working up to that time to miss them.

In the fall of 1965 I wrote up a research proposal for the NSF on the Yellowstone work, emphasizing the cyanobacteria research and the possibility



Figure 3 Getting ready for the first Yellowstone research trip, summer 1965, in my Indiana University laboratory, Jordan Hall Room 361. Three women who were to make important contributions to the Yellowstone project: Sally Murphy (foreground), Pat Holleman (left rear), and Louise Brock.

of using thermal springs as model ecosystems. This proposal was funded, and I began serious work in Yellowstone in June 1966.

The early Yellowstone research was done in temporary laboratory facilities we set up in a rented cabin. Most of this work is described in detail (21). What does not come across well in this book is my gradual realization of the broad practical implications of what I was doing. Initially I had viewed the Yellowstone hot springs primarily as model ecosystems for studying basic questions of microbial ecology. However, as I began to publish papers, I received queries from other scientists, especially biochemists, who had different interests and agendas. Because of my broad interests, I always encouraged such inquiries and arranged for samples, cultures, and even housing accommodations and research space in our Yellowstone project. After we had established the laboratory at West Yellowstone, Montana (see Figure 14.1 in Reference 21), these arrangements became not only easier, but one of my goals, as I viewed the laboratory as a generalized research facility. Also, as the years went by, I involved more of my graduate students and postdoctoral workers in the Yellowstone work, as well as key laboratory technicians and undergraduate students. The first graduate student to work on the project, and one of the most productive, was Bill Doemel (Figure 4).

Discovery of Thermus aquaticus

Most of the early work in Yellowstone focused on measurements of photosynthesis in organisms from the thermal mats and on the temperature optima of the various populations, but from the beginning I attempted to study bacteria in the higher-temperature regions where the photosynthetic organisms were absent. Hudson Freeze was an honors undergraduate student who was with us in Yellowstone the summer of 1966, and he was interested in a project he could do for his honors thesis the following year. I suggested that he try to culture the pink bacteria from Pool A (Octopus Spring). Just before leaving at the end of the summer, we collected pink bacteria as well as mat samples from several other sources, including the outflow channel of Mushroom Spring, which had a temperature of about 69°C.

I knew from my work on marine and freshwater microbiology that culture media for aquatic microbes should not be too rich in organic constituents, so we developed a medium using synthetic salts to which we added small amounts of tryptone and yeast extract. After inoculation, the cultures were incubated at 70°C in a water bath. Although we did not succeed in culturing the pink bacteria [they are still uncultivated, although their molecular phylogeny is known (45)], extensive growth of yellow-pigmented bacteria occurred with the 69°C sample from Mushroom Spring. The mat here had been very thin, near the upper temperature limit for photosynthesis, so we used a small bit of the underlying siliceous sinter (to which the organisms adhered) for the inocu-



Figure 4 Two pioneer participants in the Yellowstone project, Nancy and Bill Doemel, summer of 1967. They were actually on their honeymoon. Nancy served as a field assistant for most of Bill's early work. She later worked on my textbook, *Biology of Microorganisms*.

lum. *Thermus aquaticus* itself presumably represented only a very small amount of the microbes in the inoculum. By October 1966, Freeze had his first culture, a strain he designated YT-1. Subsequently, I isolated quite a few more strains from other sources, both in Yellowstone and in thermal areas in other parts of the world (as well as from hot water heaters!).

The work on *T. aquaticus* continued sporadically over the next two years, much of it done by Pat Holleman, a technician in my laboratory who had done extensive work on a variety of my research problems. (Pat Holleman was one of the most important people in my laboratory for several years, as can be seen by credits in various papers. She worked on yeast mating, *L. mucor*, and various Yellowstone projects from about 1964–1969. When her husband was sent to Vietnam in 1968–1969, she lived with Louise and me for about a year, both in Bloomington and West Yellowstone.) Freeze's undergraduate course load meant that his work on *T. aquaticus* tended to come in fits and starts. However, he was responsible for all of the DNA base composition work, as well as the

measurements of growth rates at various temperatures, and I ended up doing the bulk of the taxonomic work (35).

Most of the thermophilic bacteria that had been described by earlier researchers were spore-forming bacteria, whereas the new bacterium was definitely not a spore-former. In deciding on a name, I did an extensive survey of the literature of thermophilic bacteria. The name I first selected was *Caldobacter trichogenes*, but sometime after the first draft was typed I changed the name to *Thermus aquaticus*. I do not remember why. (What would Taq polymerase be called if the original name, *Caldobacter trichogenes*, had been used for this organism?)

At the time that the paper on *Thermus aquaticus* was being written, I also deposited representative cultures of the organism in the American Type Culture Collection, in Washington, DC. Among these cultures was YT-1 (ATCC 25104), which later became the source of Taq endonuclease (46) and Taq polymerase for the polymerase chain reaction (PCR). Cultures of YT-1 were passed around by Richard Roberts of Cold Spring Harbor as sources of endonuclease. Soon, *T. aquaticus* was eliciting considerable interest among microbiologists, biochemists, and molecular biologists. Throughout the 1970s, the number of papers on this bacterium continued to increase, and when PCR was reported in the mid 1980s, the reports became even more prolific. By the end of 1990 over 1000 papers on *T. aquaticus* had been published.

Bacteria in Boiling Water

Although I was convinced in 1965 that bacteria were living at much higher temperatures than had been previously suspected, I had still not realized that they were living in boiling water (i.e. at temperatures near 100°C). My ideas had been based only on observations in outflow channels with visible accumulations (such as the pink bacteria at temperatures above 80°C in Octopus Spring). However, near the end of the summer of 1967, I started using an immersion slide technique and realized that although there were no visible accumulations in the boiling pools themselves, bacteria were present in virtually every pool I examined. Although the immersion slide technique had been widely used in microbial ecology, it took me quite a while to get around to using it in boiling springs.

Because of the importance of the immersion slide technique for the discovery of bacteria in boiling water, the history of its use in Yellowstone boiling springs warrants some discussion. I had been invited by the Society of Applied Bacteriology (UK) to participate in a symposium on extreme environments that was to take place in Belfast in July 1967. I decided to present some material on high-temperature bacteria (32), so Louise and I attempted to obtain incorporation of ¹⁴C glucose into the pink bacteria to determine their temperature optimum, as we had been doing with the phototrophs. However, incorporation of the radioisotope was virtually nil, leading me to hypothesize that the visible accumulations of pink bacteria might be moribund. If so, it seemed possible that good incorporation would be possible if actively growing populations were used. To get such populations, we immersed pieces of string directly in the outflow channel, as well as in the source pool itself. We got good growth on the string in the channel, but what was really exciting was that I also saw small amounts of pink material on the string from the source pool, organisms that had obviously grown on the string during the immersion period. These observations suggested for the first time that bacteria were growing in the source pool itself, which had a temperature of over 90°C. Obviously, organisms would have been seen microscopically on the string after a shorter incubation time, so I decided to immerse microscope slides directly in the pool. Microscopic observations of a slide one day after immersion in Octopus Spring showed large numbers of filaments throughout the slide. I took photomicrographs, one of which was subsequently used in my 1967 *Science* paper (see below).

Obviously, these organisms were growing rapidly in these high-temperature systems. The upper temperature limit for bacterial growth was obviously not in the 80°C range, as I had thought, and could conceivably be much higher.

The discovery of the wide distribution of bacteria in boiling springs came about more or less by chance. On August 11, 1967, I had a visit from Anne and Jerry Mosser, who were then graduate students at Rockefeller University and were on a honeymoon trip (Jerry had been an honors undergraduate student in my laboratory in the early 1960s). When I had visitors, I usually tried to show them some interesting areas, but I also liked to do some science. What better than to carry out a widespread slide study in boiling and superheated pools? The experiment was simple: Tie one or two slides to a piece of string, drop the slides in the pool, and tie the other end of the string to a log, rock, or nail. We spent a pleasant day wandering over the Lower Geyser Basin, dropping slides in boiling pools (Figure 5).

On Sunday, August 20, all the slides were removed and returned to the laboratory for microscopy. Virtually every slide, from every boiling or superheated pool, had heavy bacterial growth readily visible microscopically. In some cases, the density was so heavy that the slides had a film visible to the naked eye. The following summer (1968) Tom Bott did an outstanding job of proving not only that growth occurred, but of actually measuring growth rates (2).

"Life at High Temperatures": the Science Paper

In early 1967, the editors of *Science* asked me to write a lead article "in the general area of microbial ecology." By this time the Yellowstone work occupied most of my thoughts, so I decided to write the paper "Life at High Temperatures," with an emphasis on my own work in Yellowstone. In fact, I

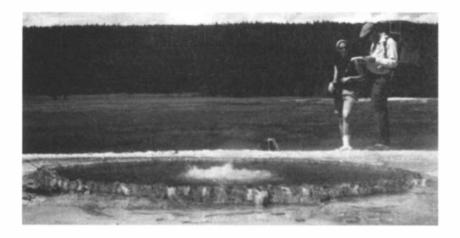


Figure 5 The first study of bacterial growth in superheated pools, using the immersion slide technique. A Mosser and TD Brock at Steep Cone, August 11, 1967.

turned eagerly to this task, and although the editor's deadline was not until June 1, I completed the article and submitted it by April 24, 1967. I had not yet discovered bacteria in boiling water (described above), but by the time the edited version was returned to me in mid August, I had already begun the extensive slide study of bacteria living in boiling and superheated pools. Thus, I had much stronger evidence for life in boiling water and published in this paper photomicrographs of organisms from the immersion slides.

This article, published in the fall of 1967 (18), elicited a lot of interest and led to several fruitful collaborations, of which the most significant was that with Mercedes Edwards, an electron microscopist at the State Laboratory of Public Health, Albany, New York. Mercedes and I worked jointly on the fine structure of several of the high-temperature bacteria, and her stunning electron micrographs greatly enhanced several publications as well as lectures that I was now giving around the world.

Travels in Search of Hot Springs

I had always loved to travel, and now I found myself in the exciting position of having valid scientific reasons for going to exotic places. Most of the geothermal regions of the world are in interesting areas: Italy, Iceland, New Zealand, Japan, Central America, the Caribbean. Over the years 1966–1972 I visited all these areas, some of them more than once.

The initial rationale for visiting such regions was to find boiling springs at lower altitudes than Yellowstone. Because of its altitude, water boils at about 92°C there. I had found bacteria in many Yellowstone boiling springs but wondered, was 92°C the upper temperature limit, or would bacteria be present at even higher temperatures? Especially in Iceland and New Zealand, the temperatures in low-altitude boiling springs range up to 100°C or a little higher in superheated waters. I found bacteria in virtually every boiling spring of neutral or alkaline pH in these areas, thus extending to a somewhat higher value the upper temperature limit for life.

All of these trips were part of other travels. In the case of Iceland, I had begun studying the new volcanic island Surtsey (see above), and return visits there (four in all) enabled me to visit springs on the mainland. My New Zealand visit was part of an extended trip prompted by an invitation to attend an international symposium on cyanobacteria in India. My Italian visits were combined with marine work I was doing on *L. mucor*.

At the time of my visits to Iceland and New Zealand, I found that the local microbiologists had neither knowledge nor curiosity about the biology of their thermal habitats. In fact, I published the first work from these countries (31, 33). Later, after the biotechnology industry had discovered thermophiles, the local scientists got interested, and both countries now have active research groups (40, 44). However, little of the present work in these regions is ecological. Mainly, it involves the study of cultures obtained from natural samples.

Deep Sea Vents

For many years my Yellowstone work seemed somewhat exotic to many microbiologists, perhaps because of the presumed restricted distribution of hot springs. This attitude changed after the discovery of the deep sea vents, with their very high temperatures and the associated diverse and flourishing life forms. After the discovery of deep sea vents in the late 1970s, my Yellowstone work took on broader significance; it not only legitimized hypotheses that microbes might be present in some of these high-temperature systems, it also provided the essential foundation for studies on the microbiology of thermal vents. The techniques and principles that we had developed for proving that bacteria live and reproduce in boiling water could be applied to the deep sea habitats. Furthermore, working in Yellowstone was much easier and cheaper, so even those interested primarily in marine thermal vents also visited Yellowstone.

Microbial Prospecting in Yellowstone

Although it was clear when I ended my project in 1975 that the Yellowstone hot springs contained many interesting organisms, it was not until the advent of PCR that widespread attention really focused on thermophiles. Not only has the biotechnology industry discovered Yellowstone, but the National Park Service itself has finally realized that Yellowstone has more of biological interest than grizzly bears and lodgepole pines (42, 43). Dozens of research groups now have permits to collect microbial samples in the park. Perhaps some of these groups will find valuable organisms, just as we found *T. aquaticus*, which led to the discovery of Taq polymerase. Never before has industry profited directly from living creatures taken from a national park, and the Yellowstone administrators are concerned about whether the Park itself should participate in the largess. "When you see the money that's being made," says Yellowstone research chief John Varley, "that's hard for a starving bureaucrat to overlook" (43).¹

Yellowstone, of course, has no monopoly on thermophiles, but it provides the most accessible location where a wide variety of thermal habitats are available.

Biology of Microorganisms

One of the most satisfying activities of my career has been the success of my textbook, *Biology of Microorganisms (BOM)* (20). I signed the contract for this book with Prentice-Hall (P-H) on January 11, 1967. Although I had already published two books (8, 14), they were both modest in scope, whereas the new book was to be a major effort, with a lot of money riding on the outcome. I had always been interested in writing, and with the broad knowledge that I had acquired since leaving graduate school, I felt capable of tackling the challenge of a major textbook. Another significant reason was the potential financial reward of a successful textbook. I had a mortgage on a house, and as a depression-era baby, I had a strong aversion to debt. A decent book would enable me to pay off this mortgage, the only debt I owed. (This proved to be true.)

From early 1967 until the fall of 1969, I spent many weekend and earlymorning hours working on this text. I did the first outline on long winter evenings at Old Faithful at the end of January 1967, while I was participating in a winter field expedition. I wrote several important chapters early in the morning at West Yellowstone, while waiting for students or technicians to assemble for a day of field work.

¹This issue, coupled with the use of Taq polymerase in DNA testing, has seemed to galvanize the news media. In addition to the articles cited, news reports have appeared in Audubon Magazine ("The Microbe Miners," December 1994), Gannett News Service ("Yellowstone's Living Lab," October 10, 1994), Los Angeles Times ("Simpson Case Boosts Microbe Conservation," August 31, 1994), Genetic Engineering News ("Biotech Finds Yellowstone National Park a Thermophilic Microbe Hotbed," March 15, 1994), High Country News ("Firms Milk Park's Wildlife," December 27, 1993), Billings Gazette ("Tiny Treasures; Yellowstone Secrets," December 5, 1993), Wisconsin State Journal ("Hot Water Bacterium; Fight over Tiny Critter Looms," May 24, 1993), London Times ("Going to Extremes," August 14, 1993), Milwaukee Journal ("Heat-Loving Bacterium Roils Two Worlds," May 9, 1993). There have also been news reports on national television.

Because P-H was investing a lot of money in the book, they were prepared to do a handsome production job, with state-of-the-art design, typography, printing, etc. The first edition of BOM was intended primarily for the so-called nonmajors market, which would have required lots of practical material, but I chose to emphasize general concepts instead. As P-H also published The Microbial World by Stanier, Doudoroff & Adelberg (46a), it was important that the two books not compete. Despite these limitations, my book proved successful, and I soon considered a new edition. However, by the time I began working on the second edition, in 1972, P-H had concluded (erroneously, as it turned out) that their other textbook was not going to be revised. Consequently, the editor, Chester Lucido, asked me to raise the level of my book so that it would serve the Stanier et al market. I happily took this opportunity to cover the material at a level I was more comfortable with. Three subsequent editions, as well as translations into Japanese and Spanish, all did very well throughout the 1970s and early 1980s. Then about 1986, I convinced P-H to permit me to completely redesign the book using new full-color art. Thus, the fifth edition of BOM, published in 1988, became the first full-color microbiology textbook on the market. By this time I had acquired an outstanding coauthor, Michael Madigan, who took over most of the writing for the revision for the sixth edition (1991), while I concentrated on the technical aspects of book production. The book, now in its seventh edition (1994), continues to be successful.

Beyond Yellowstone

At a cocktail party at the American Society for Microbiology in May 1970, someone asked me where I was from. "Indiana University," I answered. "Are you with Brock?" he queried. "No," I countered, "I *am* Brock." The conversation then ended in confusion, but it was at that point that I knew I had "arrived."

The title of my book *Principles of Microbial Ecology* was the first to address this field, and the book itself was published just before the big interest in environmental awareness. (The first US Earth Day was in the spring of 1969.) For me, the wave of enthusiasm for ecology culminated in the offer of a chair professorship (EB Fred Professor of Natural Sciences) at the University of Wisconsin-Madison (UW) in 1971. This professorship meant a lot to me, as it validated everything I had done up to that time. I had always been attracted to UW and had actually applied for admission as an undergraduate when I was discharged from the Navy in 1946. (I was denied admission because I was a nonresident.) The UW position was very attractive, and although I owed a lot to IU (which among other things had provided the seed money to start my West Yellowstone research laboratory), things had changed there since 1960, and there was no good reason for me to stay. As Jacob Henle once said, the

ROAD TO YELLOWSTONE 21

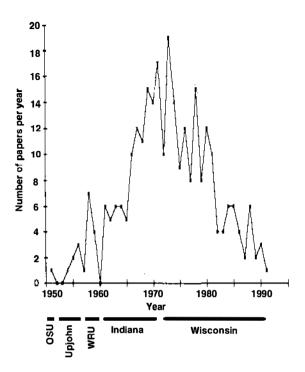


Figure 6 The trajectory of a career. The number of papers and/or books published by TD Brock each year.

only time a professor feels really independent is when he receives a call from another university. Fortunately, I was able to transfer my Yellowstone operation in its entirety. At about the same time, my personal life changed, as I married Katherine Middleton in February 1971. I never regretted the move to Madison, as I found myself in one of the top bacteriology departments in the country.

The Madison years were the most productive of my career (Figure 6). However, within a few years I started to think of other research programs besides Yellowstone. I had always been fascinated by lakes, and limnology in particular had appealed to me since my vacations in northern Ontario. The Yellowstone work continued at Wisconsin for five more years, and in fact many important studies were carried out in that time, including especially the work on the genera *Sulfolobus* and *Chloroflexus*. During this period, I had another excellent technician, Charlene Knaack. Nevertheless, I had always been fascinated with lakes, and the Wisconsin lakes kept beckoning. Also, I thought I should do something for the taxpayers of Wisconsin, who were, after

all, paying part of my salary. Finally, in the fall of 1975 I called it quits in Yellowstone and initiated a major study on cyanobacterial populations of Lake Mendota. This was fun work, and I learned lots about limnology. I also learned lots about computer programming and began to develop computer models for natural microbial populations. The work dealt not only with Lake Mendota, but with a variety of lakes throughout Wisconsin. Several major PhD theses resulted, including those of Tim Parkin, Bob Fallon, and Carlos Pedros-Alio, and the excellent postdoctoral work of Al Konopka. Eventually, the Lake Mendota work was published in a book (25) and I moved on to other things.

The work I did on lakes never elicited the excitement in others that my Yellowstone research had aroused. In contrast, the Yellowstone work continued to find interest, partly because of the work of Carl Woese on microbial evolution (50). As it turned out, several of the organisms we had discovered in high-temperature systems fell into Woese's classification as *Archaebacteria* (*Archea*). The fact that we had cultured and described these organisms made it possible, I believe, for Woese to quickly extend the *Archaebacteria* concept. Soon, other laboratories, especially the German laboratories of Wolfgang Zillig and Karl Stetter, were isolating large numbers of new extreme thermophiles, most of which were *Archaebacteria* (48). Some of this work was motivated by the discovery of the deep sea vents.

In the subsequent years, especially because the archaebacterial concept and PCR have elicited wide interest in thermophiles, I have been called upon frequently to discuss my Yellowstone work. Now, I can do it only in a historical context, but as I have become primarily a historian, this has not been difficult.

History of Microbiology

I never had a history course in college, which is perhaps why I have found history fascinating. In the 1980s I returned to the old love from my Kalamazoo days, but this time in a more involved way. My book *Milestones of Microbiology* was an early effort, done when I knew very little of microbiology itself and almost no history of the field. In retrospect, it is amazing that the book is as good as it is. I had never, however, attempted to pass myself off as a historian of microbiology. (The Preface of *Milestones* begins: "This is not a history of microbiology.")

In the late 1970s, as I felt the years passing by, I became more interested in doing the "real" history of microbiology. Historical research is a respectable scholarly activity, and something I could do without research grants, students, or technicians. I was blessed with excellent library facilities at UW. My first book, a biography of Robert Koch, made use of the German-language skills I had acquired in Kalamazoo (26). Surprisingly, there had never been a real biography of Koch in English, and my book was well received. My second book, the history of bacterial genetics (27), was more of a stretch, but the weeks I spent at Cold Spring Harbor in the summer of 1959 paid off, and this book was also received favorably. I was surprised, though, that my department did not view this work as valid research, and I was pressured to retire.

In recent years, I have returned to one of my early loves, local history, combining my expertise in book publishing with my feel for history, producing on a pro bono basis several publications for Historic Madison, Inc. In addition, I have become the unofficial historian of the Village of Shorewood Hills, where I have made my home since moving to Madison.

Computers

My interest in computers arose initially from my writing activities, but when I became involved in lakes research I also used computers in the analysis of data. I initially began with the UW mainframe computers, but when the microcomputer became available in the late 1970s, I became heavily involved with these fascinating tools. Beginning with the Apple II, then moving on to CP/M-based systems and finally to the IBM-PC, I have spent most of the 1980s and early 1990s sitting in front of a computer screen. I published numerous articles in microcomputing magazines (22, 23), learned programming languages, and wrote extensive programs. At one time in the early 1980s, I thought that I might give up microbiology and become a computer scientist, but I decided that the computer is simply a tool, in my case useful primarily for writing and publishing scientific books.

Publishing

My publishing activities arose out of my interest in computers. When I realized that a word processor file created on a microcomputer could be transferred to a typesetter and used to set type, I realized that publishing had entered a revolution. Unable to convince Prentice-Hall to use computers (this was around 1980), I decided to go into publishing myself. Taking the bull by the horns, I not only wrote a book and set the type (using a program called T_EX that was available on the UW mainframe computer), but I actually printed and published the book (24), setting up a company for marketing and sales. I chose a topic from my microbial ecology work that was sufficiently broad to engender a substantial market for the book. During this period, I was also a full-time faculty member, so my publishing activities were carried out at nights and on weekends. In this endeavor I was greatly assisted by my wife Kathie, who actually became the principal operating officer of the company.

This first book was successful and led to more. Eventually, I found myself retired from the university and running a company with its own building and nine employees. In addition to publishing our own books, we also handled production for other publishers. Out of approximately 60 titles, the most extensive project was the design, copyediting, and production of the second edition of *The Prokaryotes*, a four-volume enormity that consumed all of 1990–1991. (I am the only person in existence who has read *every* chapter in this immense undertaking!)

However, the most important part of my publishing activities is the knowledge I have gained about book design and production, printing, graphic arts, and related areas. It was with this knowledge, along with the track record I had already established, that I convinced Prentice-Hall to allow me to redesign my textbook, *Biology of Microorganisms*, as a full-color book. The ensuing success was certainly one of the most satisfying experiences of my career and topped off a very fulfilling life.

Final Words

Modern scientific research is almost always a collective activity of many people. Unfortunately, space limitations have kept me from crediting all those who have made important contributions to my own research. I list them in Table 1 (students) and Table 2 (postdoctoral associates). Technicians, except for those specifically mentioned above, are credited in specific research papers.

In reviewing my life and career, I can see that my broad interests have carried me into quite a few fields. This has been both a strength and a weakness—a strength, as many of my innovations have come from applying ideas from one field to another; a weakness, because I have had to work hard to become accepted by the workers in each field. I have occasionally thought how nice it would have been to have specialized in one narrow area (e.g. mycoplasmatology or methanogenesis). I could have published in only one or a few journals, gone to one type of meeting, interacted with a just handful of laboratories around the world. Collegiality stands for a lot in science, and it takes quite a while to build up a reputation in a given field. As it was, every time I switched arenas I had to qualify myself with a new set of peers. Peer groups often operate like closed corporations, and working one's way in is difficult, sometimes impossible.

I made a list of the various groups to which at one time or another I contributed. The count was 32! Many of my colleagues were completely unaware of my associates or even activities in other fields.

Certain key choices have led me to where I am today. Some of them were made with serious deliberation, whereas some of the most important were made casually. However, the things I have not done account for where I am today as much as what I have done. These negative decisions do not end up in a narrative such as this, but I know that I came within a whisker, several times,

ROAD TO YELLOWSTONE 25

Student name	Dates in lab	Research topic	
Allen, Stephen D	1966–1967	Temperature optima of intestinal microflora (Master's)	
Bauld, John	1970–1972	Chloroflexus mats	
Bland, Judith	1970–1971	Leucothrix as an algal epiphyte	
Clyne, Jenny	1981 – 1982	Bacterial utilization of algal excretion products (Master's)	
Crandall, Marjorie	1965 - 1967	Biochemical basis of mating in yeast	
Davie, Joseph M	1963 - 1965	Bacteriocine/hemolysin of group D streptococci	
Delmer (Pierson), Deborah	1962 - 1963	Bacteriocines of group D streptococci (under- graduate)	
Doemel, William	1967 – 1970	Physiological ecology of Cyanidium	
Entenmann (Cook), Susan	1974	Sulfolobus ecology (undergraduate)	
Fallon, Robert	1976 - 1980	Cyanobacteria in Lake Mendota	
Fliermans, Carl	1969 - 1971	Ecology of hot acid soils	
Freeze, Hudson	1966 - 1969	Thermus aquaticus/thermostable aldolase (un- dergraduate)	
Gustafson, John	1975 – 1976	Ferric iron as an electron acceptor by sulfur bac- teria (undergraduate)	
Herdrich, Gary	1974	Temperature optima of bacteria from cold habitats (undergraduate)	
Hoffman, James	1973–1974	Thermal pollution of Madison lakes (under- graduate)	
Kelly, Michael	1966-1968	Physiological ecology of Leucothrix	
Lay, Bibiana	1982	Long-term changes in phytoplankton in Wisconsir lakes	
Madigan, Michael	1973–1976	Ecology and physiology of Chloroflexus	
Moo-Penn, Gloria	1961	Amino acid transport in group D streptococci (undergraduate)	
Mosser, Jerry	1962 - 1964	Streptococcus phage/Leucothrix (undergraduate)	
O'Dea, Katherine	1976	Ferrous sulfide as a redox agent for anaerobes (undergraduate)	
Parkin, Timothy	1976 - 1980	Ecology of phototrophic bacteria in lakes	
Passman, Fred	1969-1970	Ecology of cold springs (undergraduate)	
Pedros-Alio, Carlos	1977 - 1980	Bacterioplankton ecology	
Peterson, Sandra	1973 – 1975	Chloroflexus/halophilic bacteria (undergraduate)	
Ray, Paul	1967 – 1970	Lipids and membranes of Thermus aquaticus	
Remington, Patrick	1973 – 1975	Microbial mats in Yellowstone (undergraduate)	
Smith, David	1970–1972	Water relations of Cyanidium in hot acid soils	
Vidaver, Anne	1962–1966	Biochemistry of phage receptor of Streptococcus faecium	
Ward, David	1972–1975	Hydrocarbon decomposition in lakes	
Weiss, Richard	1970–1971	Fine structure of Sulfolobus	
Weller, Donald	1974	Stromatolitic structures of <i>Phormidium</i> (under- graduate)	
Zeikus, J Gregory	1969-1970	Protein synthesis at high temperature	
Zinder, Stephen	1974 - 1977	Organic sulfur compounds in thermal and aquatic environments	

 Table 1
 Students receiving the PhD or whose work led to published papers

Name	Dates in lab	Research topic
Belly, Robert	1970 1973	Thermoplasma ecology; acidothermophiles; coal mining ecology
Bohlool, Ben	1972-1973	Sulfolobus and Thermoplasma ecology
Bott, Thomas	1968 - 1969	Growth rates of bacteria in boiling springs
Boylen, Charles	1971 - 1972	Firehole River ecology
Darland, Gary	1969 - 1970	Acidothermophile ecology; Thermoplasma
Doemel, William	1973 - 1975	Growth and decomposition of microbial mats
Ingvorsen, Kjeld	1979 – 1980	Sulfate reduction in Lake Mendota
Johnson, Roy	1963 - 1964	Streptococcus phage
Konopka, Alan	1975 - 1977	Cyanobacteria ecology in lakes
Leon, Shalom	1965 - 1966	Interaction of streptomycin with ribosomes
Lynn, Raymond	1968	Zygogonium in acidothermophilic habitats
Middleton (Brock), Katherine	1970–1971	Sulfolobus and Thermoplasma ecology
Mosser, Jerry	1970–1974	Yellowstone ecology; ecology of high-alpine habitats
Shivvers, Douglas	1971 – 1 <u>9</u> 72	Metabolism of sulfur by Sulfolobus
Tansey, Michael	1970–1 <mark>97</mark> 1	Thermophilic fungi
Watson, Vicki	1981 1983	Modeling cyanobacterial populations in Lake Mendota
Zehnder, Alexander	1978 - 1980	Anaerobic methane oxidation
Zeikus, J Gregory	1970	Firehole River ecology

Table 2 Postdoctoral associates

of going off in what would have been a professionally fatal direction. As always, neither hard work nor brilliance can substitute for good luck.

The recent interest in Taq polymerase and *T. aquaticus* has brought my earlier work to the attention of a new generation of scientists and the public. The managers of Yellowstone National Park have called on me once more to provide new material for their interpretive programs, and in 1994 I wrote a work called *Life at High Temperatures*, a small book in which I could use some of the now historic color photographs that I had taken over the years (29). It was indeed a pleasure to revisit scenes of former research activities and to think again about those exciting days in the late 1960s when every study we carried out in Yellowstone led to new discoveries. I have also developed an interest in the history of Yellowstone Park itself and have begun a major collection of early reports, photographs, paper ephemera, and guidebooks relating to the history and development of the Park. Who knows—eventually this collection may lead to another book on Yellowstone!

The Road to Yellowstone was never straight, but it was almost never bumpy, and the view was marvelous all the way.

Any Annual Review chapter, as well as any article cited in an Annual Review chapter, may be purchased from the Annual Reviews Preprints and Reprints service. 1-800-347-8007; 415-259-5017; email: arpr@class.org

Literature Cited²

- 1. Bland JA, Brock TD. 1973. The marine bacterium *Leucothrix mucor* as an algal epiphyte. *Marine Biology* 23:283-92
- Bott TL, Brock TD. 1969. Bacterial growth rates above 90°C in Yellowstone hot springs. Science 164:1411-12
- Brock TD. 1951. Studies on the nutrition of Morchella esculenta Fries. Mycologia 43:402-22
- Brock TD. 1955. Paw Paw versus the railroads. Michigan History 39(June): 129-82 plus map; 1955. Addendum, Vol. 39(September)
- 5. Brock TD. 1956. Lipid synthesis in Hansenula anomala. Mycologia 48:337-44
- Brock TD. 1956. Studies on the mode of action of novobiocin. J. Bacteriol. 72:320-23
- Brock TD. 1959. Biochemical basis of mating in yeasts. Science 129:960-61
- Brock TD. 1961. Milestones in Microbiology. Englewood Cliffs, NJ: Prentice-Hall
- Brock TD. 1961. Physiology of the conjugation process in the yeast Hansenula wingei. J. Gen. Microbiol. 26: 487-98
- Brock TD. 1964. Host range of certain virulent and temperate bacteriophages attacking group D streptococci. J. Bacteriol. 88:165-71
- 11. Brock TD. 1964. Knots in Leucothrix mucor. Science 144:870-72
- Brock TD. 1965. Biochemical and cellular changes occurring during conjugation in *Hansenula wingei*. J. Bacteriol. 90:1019-25
- Brock TD. 1965. The purification and characterization of an intracellular sex-specific mannan protein from yeast. Proc. Natl. Acad. Sci. USA 54: 1104-12
- 14. Brock TD. 1966. Principles of Microbial Ecology. Englewood Cliffs, NJ: Prentice-Hall
- Brock TD. 1966. Streptomycin. In Biochemical Studies of Antimicrobial Drugs. 16th Symposium Society for General Microbiology, pp. 131-68. Cambridge: Cambridge Univ. Press
- Brock TD. 1966. The habitat of Leucothrix mucor, a widespread marine microorganism. Limnol. Oceanogr. 11: 303-7
- 17. Brock TD. 1967. Bacterial growth rate

in the sea: direct analysis by thymidine autoradiography. Science 155: 81-83

- Brock TD. 1967. Life at high temperatures. Science 158:1012-19
- 19. Brock TD. 1967. The ecosystem and the steady state. *BioScience* 17:166-69
- Brock TD. 1970. Biology of Microorganisms. Englewood Cliffs, NJ: Prentice-Hall
- Brock TD. 1978. Thermophilic Microorganisms and Life at High Temperatures. New York: Springer-Verlag. 465 pp.
- Brock TD. 1980. Hard copy for apple graphics. *Microcomputing* November: 100-2
- Brock TD. 1980. The microcomputer in microbiology. ASM News 46:171-73
- Brock TD. 1983. Membrane Filtration: a User's Guide and Reference Manual. Madison, WI: Science Tech/Heidelberg: Springer-Verlag. 381 pp.
 Brock TD. 1985. A Eutrophic Lake:
- Brock TD. 1985. A Eutrophic Lake: Lake Mendota, Wisconsin. New York: Springer-Verlag
- Brock TD. 1988. Robert Koch. A Life in Bacteriology and Medicine. Madison, WI: Science Tech/Heidelberg: Springer-Verlag
- Brock TD. 1990. The Emergence of Bacterial Genetics. Cold Spring Harbor, NY: Cold Spring Harbor Lab.
- Brock TD. 1992. Research on thermophiles: a memoir. In *Thermophiles: Sci*ence and Technology, Int. Conf., Reykjavik, Iceland, 23-26 August 1992, pp. A3-A12. Reykjavik: IceTec
- Brock TD. 1994. Life at High Temperatures. Yellowstone Natl. Park, WY: Yellowstone Assoc.
- Brock TD, Brock ML. 1959. Similarity in mode of action of chloramphenicol and erythromycin. *Biochim. Biophys.* Acta 33:274-75
- Brock TD, Brock ML. 1966. Temperature optima for algal development in Yellowstone and Iceland hot springs. *Nature* 209:733-34
- Brock TD, Brock ML. 1968. Relationship between environmental temperature and optimum temperature of bacteria along a hot spring thermal gradient. J. Appl. Bacteriol. 31:54-58
- 33. Brock TD, Brock ML. 1971. Microbio-

²Because of space limitations, my own publications in this bibliography are incomplete. A copy of the complete one will be sent to any interested reader.

logical studies of thermal habitats on the central volcanic region, North Island, New Zealand. NZ J. Mar. Freshwater Res. 5:233-57

- Brock TD, Davie JM. 1963. Probable identity of a group D hemolysin with a bacteriocine. J. Bacteriol. 86:708-12
- Brock TD, Freeze H. 1969. Thermus aquaticus gen. n. and sp. n., a nonsporulating extreme thermophile. J. Bacteriol. 98:289-97
- Brock TD, Peacher B, Pierson D. 1963. Survey of the bacteriocines of enterococci. J. Bacteriol. 86:702-7
- Brock TD, Wooley SO. 1963. Streptomycin as an antiviral agent: mode of action. Science 141:1065–67
- Brock TD, Wooley SO. 1964. Glycylglycine uptake in streptococci and a possible role of peptides in amino acid transport. Arch. Biochem. Biophys. 105: 51-57
- Crandall MA, Brock TD. 1968. Molecular aspects of specific cell contact. Science 161:473-75
- Geirsdottir AM, Brown HP, Skjenstad T. 1992. Thermophiles: Science and Technology. Int. Conf., Reykjavik, Iceland, 23-26 August 1992. p. 112. Reykjavik: IceTech
- Kelly MT, Brock TD. 1969. Physiological ecology of Leucothrix mucor. J. Gen. Microbiol. 59:153–62

- 42. Milstein M. 1994. There's gold in them thermophiles. *Outside* August:22
- Milstein M. 1994. Yellowstone managers eye profits from hot microbes. Science 264:655
- 44. Reeve JN. 1994. Thermophiles in New Zealand. ASM News 60:541-45
- Reysenbach A-L, Wickham GS, Pace NR. 1994. Phylogenetic analysis of the hyperthermophilic pink filament community in Octopus Spring, Yellowstone National Park. Appl. Environ. Microbiol. 60:2113-19
- Sata S, Hutchison CA, Harris JI. 1977. A thermostable sequence-specific endo nuclease from *Thermus aquaticus*. Proc. Natl. Acad. Sci. USA 74:542-46
- 46a. Stanier RY, Doudoroff M, Adelberg EA. 1957. The Microbial World. Englewood Cliffs, NJ: Prentice-Hall
- wood Cliffs, NJ: Prentice-Hall
 47. Stanier RY, Doudoroff M, Adelberg EA. 1957. See Ref. 46a, p. 294
- Stetter KO. 1986. Diversity of extremely thermophilic archaebacteria. In *Thermophiles. General, Molecular, and Applied Microbiology*, ed. TD Brock, pp. 39–74. New York: Wiley
- Vidaver AK, Brock TD. 1966. Purification and properties of a bacteriophage receptor material from *Streptococcus* faecium. Biochim. Biophys. Acta 121:298-314
- 50. Woese CR, Wolfe RS, eds. 1985. Archaebacteria. New York: Academic