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Professor Dr Dr h.c. mult. Otto Kandler: distinguished botanist and microbiologist

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It is a great privilege to write a short biography of my PhD supervisor and long-time mentor, Otto Kandler (Figure 1).

Difficult path to a remarkable career

Otto Kandler was born on 23 October 1920 in Deggendorf, Bavaria. His father was a professional gardener. Growing up and helping in his father's market garden, Otto Kandler became interested in plant life and biology in general. He had read about Darwin when he was twelve years old and mentioned it to a catholic priest. The priest punished him with two strikes on his hands with a rod. This memorable incident may have been the reason for Otto Kandler's continuous interest in the origin and evolution of life (Kandler, 1979, 1987).

As a very young man he wanted to follow in the footsteps of his dad but the Second World War interfered with his intentions. He had to join the German army as a radio reporter on the Russian Front. At the end of the war he was in Austria and escaped by bicycle to the Western Front to avoid capture by the Russians. After spending a few months in an American prison camp he was allowed to return home. By then, he was eager to study biology but in the post-war confusion it was difficult for students. Much of the university of Munich had been bombed and the students had to help to remove rubble from the ruins. There were no scholarships available and students had to find other ways to pay for their education. Nevertheless, in 1946 he enrolled in botany, zoology, chemistry, and physics at the Ludwig-Maximilians-University in Munich and financed his studies by growing and selling cabbage and flowers in Deggendorf. He majored in botany and, in order to study metabolism and the effect of auxin, he started to grow plant tissue cultures, at that time a rather new field (Kandler, 1948; 1950). He received his doctor's degree with honors in 1949 (Kandler, 1950a). From 1949 till 1957 he was Assistant Professor of botany at the University in Munich and finished his "Habilitation" in 1953. Plant physiology was his major research topic but – already at that time - he showed some interest in bacteria. In particular, the presence or absence of cell walls in bacteria caught his interest. He convinced a young student, Gertraud Schäfer, to do her doctorate under his supervision on L-form bacteria and pleuro-pneumonia-like organisms (PPLOs). The PPLOs, which are wall-less, penicillin-resistant bacteria, are now classified as mycoplasmas. Gertraud finished her doctorate with great success, and soon became his wife and mother of three daughters. The two of them published cutting-edge papers on the proliferation of PPLOs and L-form bacteria by a budding process (Kandler and Kandler, 1954, 1955; 1956; Kandler et al., 1954). Even now, after more than 50 years, these publications are still of interest for recent research projects (Leaver et al., 2009). Gertraud and Otto Kandler have been happily married for almost 60 years.

Figure 1. Otto Kandler in 1976.

Plant physiology

Otto Kandler was very interested in plant-growth-promoting factors (Kandler, 1952) and photosynthesis (Kandler, 1950b). He presented for the first time experimental

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evidence of photophosphorylation using *Chlorella* cells (Kandler, 1950b, 1954, 1955) and this was the reason he was offered a Rockefeller Fellowship (1956–1957). At that time, radioactively labeled compounds were not available in Germany. Therefore, he decided to join the laboratories of Martin Gibbs and Melvin Calvin in Berkeley, where he was able to use labeled compounds for his experiments. He enjoyed working in California. He told me once that the blue skies and the pleasant ambient temperature were ideal to work in the laboratory. Together with Martin Gibbs he published two important papers on the formation of sugars as subsequent products of the Calvin Cycle (Kandler and Gibbs, 1956; Gibbs and Kandler, 1957). Later on, he and his group studied the biosynthesis and physiological function of plant-specific oligosaccharides such as apiose, hamamelose, stachyose, umbelliferose, selaginose and verbascose (Kandler and Hopf, 1980, 1982). He continued his research on photosynthesis (Tanner et al., 1969; Klob et al., 1972).

At the end of his career he was a fierce opponent of the so-called "Waldsterben" (forest dieback), initiated through a hysterical discussion that started in Germany in the early 1980s (Kandler, 1990). There was an ongoing, quite emotional discussion about the state of the German forest. He had been publically discredited and even personally insulted despite his convincing scientific arguments that forest diebacks had already occurred in former times. Therefore, he was quite pleased that the world-known philosopher Karl Popper supported his critical attitude towards the "green saga of Waldsterben" (Popper's phrase) in an interview with the German magazine *Spiegel* in 1990.

Professional career

Upon his return from the United States he was dissatisfied with the poor laboratory conditions at the university and was glad to find an opportunity to become director of the Bacteriological Institute of the South German Dairy Research Center in Freising-Weihenstephan in 1957. This was actually a brave decision since he had no inkling of dairy microbiology but soon he developed an interest in applied microbiology and biotechnology that he maintained throughout his career.

In 1960, he was appointed Full professor and Head of the Department of Botany of the Technical University Munich and simultaneously maintained his position as director of the Bacteriological Institute in Freising. It was convenient for me since I was living in Freising and did not have to take the train to Munich to do my diploma and doctoral thesis under the supervision of Otto Kandler. The disadvantage, however, was that the only time to meet him and discuss scientific matters was on weekends, mainly ~~on~~ late on Saturday afternoons or Sunday mornings.

Figure 2. Otto and Gertraud Kandler during the conferral ceremony of the honorary doctorate at the Technical University of Munich (1985).

In 1968, he was appointed Full professor and Head of the Department of Botany of the Ludwig-Maximilians University and stayed there until his retirement in 1985. He was an honorary member of the German Society of Hygiene and Microbiology. He was both Dean of the Faculty of General Sciences (TUM 1962) and of the Faculty of ~~Biology~~ (LMU 1973). From 1969 to 1976 he was a member of the Senate of the German Science Foundation (DFG). From 1983 to 1988 he was Chairman of the Scientific Advisory Board of the National Research Center of Biotechnology in Braunschweig. He was also the prime mover for the foundation of the German Collection of Microorganisms and the founder as well as the Editor-in-Chief of *Systematic* and *Applied Microbiology* and served for a long time on the editorial board of Archives of Microbiology and Zeitschrift für Pflanzenphysiologie. He was elected to the German National Academy of Sciences (Leopoldina) in 1970 and to the Bavarian Academy of Sciences in 1982. He received the Bergey Award in 1982 and the Ferdinand Cohn Medal of the German Society of Hygiene and Microbiology (DGHM) in 1989. He received honorary doctoral degrees from the University Ghent (Belgium) in 1981 and from the Technical University Munich in 1985 (Figure 2). [2005: Bayerischer Verdienstorden]

He is an honorary member of the Association of General and Applied Microbiology, the largest microbiological society in Germany. He had several opportunities to move to other positions outside of Bavaria but he never accepted. He

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is tightly connected to his homeland and the following quotation may come close to his attitude: *Extra Bavariam nulla vita est, et si est vita, non est ita* (There is no life outside of Bavaria, and if yes, not this one). [Esting, Schlossmauer, Lüftlmalerei um 1920]

Otto Kandler's professional profile creates the impression that his major interests are botany. However, his scientific activities were much broader and certainly had an influence on his teaching activities. He called himself a biologist. Therefore, he taught, not only general botany and plant physiology, but also ecology, food microbiology and bacterial taxonomy (Figure 3). His broad scientific interests can be easily judged from the titles of his 400 publications. The topics range from plant tissue cultures, plant physiology, photosynthesis, plant oligosaccharides, bacterial cell walls, physiology of bacteria, applied microbiology to "Waldsterben" and origin of life and evolution. However, it has to be mentioned that about two thirds of his publications deal with microbiological aspects. Kandler's broad scientific activities are also reflected by the fact that four of his former PhD students or coworkers were appointed as full professors of botany and 13 as microbiologists (H.H. Martin, H.J. Kutzner, R. Plapp, A. Böck, K.H. Schleifer, M. Teuber, K.-O. Stetter, W. Hammes, W. Holzapfel, F. Fiedler, H. König, J. Winter, and R. Hensel).

The chemical composition of bacterial cell walls

Otto Kandler was one of the first scientists who studied the cell wall of bacteria. Already in 1958 he published a paper in *Nature* on the cell-wall composition of *Proteus vulgaris* (Kandler et al., 1958) and of other bacteria (Kandler and Hund, 1959). Later on he investigated the inhibiting effects of penicillin and cycloserine on the biosynthesis of bacterial cell walls (Rau-Hund and Kandler, 1962; Plapp and Kandler, 1965a, 1965b). Subsequent to the design and development of a simple method for the determination of the primary structure of peptidoglycan (Schleifer and Kandler, 1967), most of the currently known peptidoglycan types were described by Kandler's group (see Schleifer and Kandler, 1972). They also studied the exogeneous and endogenous effects on the modification of peptidoglycan (Schleifer et al., 1975) and the biosynthesis of peptidoglycan (Hammes and Kandler, 1976). In 1977, Kandler and Hippe described the lack of peptidoglycan in *Methanosarcina barkeri.* This was the beginning of his interest in archaeal research (see below).

Bacterial physiology

Kandler's interest in plant biochemistry and physiology also had an impact on his bacteriological studies. Already in 1956, he determined the amino acid composition of hydrolysates of bacteria by paper chromatography (Kandler and Zehender, 1956). At the same time, he carried out comparative studies on the metabolism of nucleic acid and respiration of *Proteus vulgaris* and pleuropneumonia-like organisms (Kandler et al., 1956) as well as studies on the physiology of *Caulobacter* (Hund and Kandler, 1956). In 1961, he published in Nature a study on the biosynthesis of acetoin by *Leuconostoc citrovorum.* (Kandler and Busse, 1961). He was also interested in the carbohydrate metabolism of lactic acid bacteria (Weiss et al., 1968, Stetter and Kandler, 1973, Kandler, 1983), cellulomonas (Stackebrandt and Kandler, 1980) and bifidobacteria (Lauer and Kandler, 1976).

Figure 3. Digging up a soil profile for the students.

Taxonomy of bacteria

Otto Kandler had a strong interest in the systematics of plants and especially of bacteria (Kandler and Schleifer, 1980). Already in 1959 he proposed that the amino acid composition of the cell walls of bacteria may be used for the differentiation of bacteria in dairy products (Kandler et al., 1959). Subsequently, he dealt with the classification of staphylococci and lactobacilli (Abo-Elnaga and Kandler, 1965; Kandler, 1967a). He described new species of lactobacilli (Lauer and Kandler, 1980; Weiß et al., 1981; Kandler et al., 1983a, 1983b; Kandler and Kunath, 1983), streptococci (Collins et al., 1983, 1984), cellulomonas (Stackebrandt and Kandler 1979, 1980), acetomicrobia (Soutschek et al., 1984) and bacilli (Scholz et al., 1987). He also made important contributions to the taxonomy of bifidobacteria (Kandler and Lauer, 1974; Lauer and Kandler, 1983). In 1967, he recognized that the amino acid sequence of the peptidoglycan (murein) of the bacterial cell wall is a valuable chemotaxonomic marker (Kandler, 1967b). A little later, the different peptidoglycan types and their taxonomic implication were described in a

review in more detail (Schleifer and Kandler, 1972). By the way, this review is a citation classic and one of the most cited papers in bacteriology (more than 2500 times cited). He also wrote a review on the evolution of the systematics of bacteria (Kandler, 1985a) and coauthored a study on the phylogenetic relationship of the genera *Thermus* and *Deinococcus* (Hensel et al., 1986).

Applied microbiology and biotechnology

Louis Pasteur was one of Kandler's scientific heroes. I still can remember two quotes of Pasteur he mentioned to me at several occasions and which are characteristic of his attitude. "Where observation is concerned, chance favors only the prepared mind" and "there are no such things as *applied sciences*, only applications of science". Therefore, he was always full of ideas to exploit his scientific findings. During his tenure as director of the Bacteriological Institute of the South German Dairy Research Center in Freising-Weihenstephan he focused on dairy microbiology. He studied the shelf-life of milk that was heated under different conditions (Kandler, 1960), designed new methods for checking the quality of raw milk (Kandler, 1961), dealt with failures during the production of yoghurt (Kandler and Frank, 1963), studied the effect of bacteria content on the quality of raw milk (Kandler, 1964a) and the utilization of *Lactobacillus acidophilus* as starter culture for dairy products (Kandler, 1964b) as well as the percentage of L(+)- and D(−)-lactic acid in samples of yoghurt (Kunath and Kandler, 1980). He holds different patents on starter cultures for the production of fermented milk and vegetable (Sauerkraut) products. He also proposed methods for successfully combating micro-organisms in cooling water systems (Kandler, 1966). In 1967, he published a review on the taxonomy and technological importance of lactobacilli (Kandler, 1967). Moreover, he investigated conditions for the killing of bacterial spores at ultra-high temperature (Miller and Kandler, 1967). Later on he conducted research on thermophilic methanogens and their ability to produce methane (biogas) from sewage and other waste. For instance, he investigated the efficiency and stability of methane formation of wastes at mesophilic and thermophilic temperatures (Kandler et al., 1983) and wrote a review on archaebacteria and their biotechnological implications (Kandler, 1985b).

The founder of archaebacterial research in Germany

In my opinion, the launching of archaebacterial research in Germany was probably the most successful and far-reaching decision in his outstanding scientific career. He was the first scientist outside the United States who recognized the future importance of archaebacterial research. Based on his interest in bacterial cell walls (see above), he and his group analyzed the cell walls of extreme halophiles (Steber and Schleifer, 1975) and of *Methanosarcina barkeri* (Kandler and Hippe, 1977). Both organisms lacked peptidoglycan, a unique component of the bacterial cell wall. During this time Marvin Bryant was visiting Kandler in Munich. They had planned a joint research project on the cell-wall composition of other methanogenic bacteria. While Marvin Bryant was sitting in Otto Kandler's office, a letter from Ralph Wolfe arrived reporting from Carl Woese's exciting results on the unique phylogenetic position of methanogenic bacteria within prokaryotes. In 1976, Kandler wrote to Wolfe and mentioned that methanogens and halophiles may be "ancient relics" that have branched off from the bulk of the prokaryotes before peptidoglycan had been "invented". He asked Wolfe to send him lyophilized cells of methanogens for analyzing their cell walls. In January 1977, Kandler attended a Gordon Conference on bacterial cell walls in Santa Monica and visited Ralph Wolfe in Urbana on his way back to Germany. It was the first time Kandler met Carl Woese and learned about his results of the comparative cataloguing of 16S rRNA and their phylogenetic implications. Kandler was deeply impressed. When he returned from the United States he was very excited and told his co-workers that he has met "the Darwin of the 20th century" (Figure 4). He was convinced that research on *Archaebacteria* had a great future and he was successful in persuading the German research organization to support special research projects for this group of organisms. This was the beginning of a success story on archaebacterial research in Germany with many scientists involved such as August Böck, Gerhard Gottschalk, Karl Otto Stetter, Ralf Thauer and Wolfram Zillig, just to name a few.

In contrast to the United States, where archaebacterial funding was quite poor, this kind of research expanded quickly in Germany due to Otto Kandler's strenuous efforts. He organized the first meeting on archaebacteria in Munich in 1978 and also the first international workshop on archaebacteria in 1981. Woese's participation in these meetings was an important impulse for further research on archaebacteria in Germany. Twelve professors from across Germany attended the meetings. Woese was met with fanfare and a brass band when he arrived in Munich. Lectures of these meetings were published as special issues of *Systematic and Applied Microbiology*, a journal that was launched by Kandler in 1977. Woese was so impressed by Kandler's activities and efforts that he wrote to Wolfram Zillig in 1979 "Munich will soon be even more famous as the world capital for archaebacterial research than for its beer" and "a bit of my heart still remains in München" (Sapp, 2009).

Figure 4. Carl Woese, Ralph Wolfe and Otto Kandler (from left to right) relaxing after a hike in the Bavarian alps (1981).

A long-lasting friendship developed between Otto Kandler and Carl Woese. Woese called it a "complementary relationship". A close collaboration evolved. The Urbana group analyzed the 16S rRNA gene sequences of bacteria and archaebacteria, whereas the Munich group studied their cell-wall composition. (Kandler and König, 1978). The chemical structure of the unique pseudomurein was elucidated (König and Kandler, 1979a, 1979b; König et al., 1982) and its biosynthesis investigated (König et al., 1989; Hartmann et al., 1989).

To further improve the collaboration with the Urbana group, Erko Stackebrandt, a former PhD student of Kandler, joined Carl Woese's laboratory in 1978 where he spent a very productive year as a postdoc. Upon his return from Urbana, Stackebrandt got a position as a research associate at the Department of Microbiology at the Technical University of Munich and introduced and improved the16S rRNA technology together with Wolfgang Ludwig.

Otto Kandler, Carl Woese and Wolfram Zillig began a persistent mutual discussion about the relationship among the *Archaebacteria*, *Eubacteria* and *Eucarya*. In particular, Zillig's studies on RNA polymerases supported the fundamental uniqueness of archaebacteria (Zillig et al., 1982). In 1990, Kandler recommended shortening the names of the three groups. After long debates Kandler and Woese agreed to name them *Archaea*, *Bacteria* and *Eucarya.* However, there was still no decision about what to call the taxonomic level. Several proposals were considered, e.g. empire, realm, urkingdom or domain. Finally, they agreed on the term domain (Woese et al., 1990). As mentioned before, Otto Kandler was also very interested in the early evolution of life and in one of his last papers he rejected the existence of a common "first cell" (often referred to as LUCA – last universal common ancestor). He postulated that each of three domains of life had its own progenitor cell which originated from a "multiphenotypical population of pre-cells" (Kandler, 1994).

Résumé

Otto Kandler, Professor Emeritus of Botany at the Ludwig-Maximilians-University Munich is an internationally well-known, highly respected scientist and one of the most outstanding microbiologists in Germany. He had a tremendous enthusiasm for research on a wide variety of different topics, both in microbiology and plant physiology. In microbiology, he is particularly well known for his work on bacterial and archaeal cell walls and their implication on taxonomy and phylogeny. He was the first scientist who recognized the importance of cell-wall composition for the differentiation of *Bacteria* from *Archaea* and initiated the successful funding of research on *Archaea* in Germany. Moreover, he was also interested in the physiology and biochemistry of several groups of bacteria, especially lactic acid bacteria as well as food microbiology and biotechnology such as the optimization of biogas production under mesophilic and thermophilic conditions. He was a dedicated and extremely hard-working scientist and had the ability to fill his students with his enthusiasm for research. Therefore, it is not surprising that many of his former students and co-workers advanced to leading positions in the field of microbiology. Much of Otto Kandler's life was shared with his caring wife and former PhD student, Gertraud, who is equally enthusiastic about science as her husband, and their three beloved daughters. Despite his numerous activities he always had an open ear for his family.

Although he was strong-willed, his concern for fairness, thoroughness, and pride in accomplishment governed his behavior in every personal and professional situation. He had exceptionally high standards of performance and his gift for scientific analysis was more than a match for any problem. He was an extremely acute and reliable critic and reporter of both scientific matters and human affairs. It is not often that one has the opportunity to share the joy of experiences of science with someone who feels the same way. I was fortunate to have had Otto Kandler as a mentor and spiritual father. He is a remarkable individual, and he left his mark not only on science, but on all those who interacted with him.

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