REVIEW ARTICLE

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Herman Jan Phaff: professor, mentor, friend and colleague

Received: 5 May 2003 / Accepted: 5 June 2003 / Published online: 19 July 2003 \circledcirc Springer-Verlag and SEM 2003

Abstract Herman Jan Phaff, the father of yeast ecology, was born in the Netherlands in 1913. In his early years, he spent much time in his family's winery, which sparked his interest in microbes. Trained in the famous Delft tradition, Phaff discovered many unrecognized ecological niches of yeast, such as shellfish, rabbit stomach, frass of bark beetles, tree exudates, cactus roots, Capri figs, sewage, Drosophila flies and shrimp. He is also remembered for his pioneering work on the coevolution of yeasts, insects and plants as well as for his work on yeast β -glucanase, which resulted in major advances in the understanding of the nature of the yeast cell wall. Phaff's legacy includes research on pectin degradation by fungal enzymes and the application of molecular approaches to yeast systematics. He discovered and described many yeasts, such as the yeast named in his honor, Phaffia rhodozyma, which led to the establishment of a very important industrial fermentation process yielding high concentrations of the pigment astaxanthin, used throughout the world to provide a natural source of this important carotenoid.

Keywords *Phaffia rhodozyma* · Yeast morphology and physiology · Yeast ecology and systematics · Herman J. Phaff (1913–2001)

Introduction

Herman Jan Phaff was born in the Netherlands in 1913. In his early years, he spent much time in his family's winery, which sparked his interest in microbes. As a

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pectic acid column even before the announcement of the discovery by others of this major technique. His studies on yeast pectic enzymes led the way to the discovery by

John L. (Jack) Etchells' USDA group at North Carolina State University that cucumber softening during lactic fermentation was caused by yeasts entering the fermentation vats on the vegetables. As a student in both Herman's and Jack's laboratories, I was pleased to have participated in this commercially important research.

A major accomplishment of Herman's was the discovery, with R. Whelton, of nonrespiratory mutants of *Saccharomyces cerevisiae*, some 6 years before Boris Ephrussi's well known publication. Another important contribution was Herman's work on yeast β -glucanase, which resulted in major advances in understanding the nature of the yeast cell wall.

Working with yeasts

Herman is the father of yeast ecology. Trained in the famous Delft tradition, he discovered many previously unrecognized ecological niches of yeast, such as shellfish, rabbit stomach, frass of bark beetles, tree exudates, cactus roots, Capri figs, sewage, *Drosophila* flies and shrimp. He is remembered for his pioneering work on the coevolution of yeasts, insects and plants, being the first to establish that particular yeast species growing in the sap of trees in the Sierra Mountains of California determine the species of *Drosophila* inhabiting the tree. His work on the yeast inhabiting cactus is recognized worldwide as a major achievement in microbial ecology.

Herman was a world authority on yeast morphology, physiology and taxonomy. He was the first to discover and describe many yeasts, of which two species and one genus were named in his honor. He and his student Sally Meyer were the first microbiologists to use the tools of molecular biology to delineate yeast species and to establish evolutionary relationships among these species. This effort was recognized by his UC-Davis Faculty Research Lectureship Award in 1969, at which time, he presented the lecture "Changing Aspects in Yeast Systematics".

Herman's discovery of the yeast named in his honor, *Phaffia rhodozyma*, led to the establishment of a very important industrial fermentation process yielding high concentrations of the pigment astaxanthin, used throughout the world to provide a natural source of this important carotenoid. Astaxanthin is of great use in salmon aquaculture to provide the pink color expected by consumers of this fish. Yeast workers worldwide appreciated his book "The Life of Yeasts", written in 1966 in collaboration with Emil Mrak and colleague Marty Miller. A second revised and enlarged edition was published in 1978 and was later translated into Japanese by Susumu Nagai.

Through Herman's efforts, the Davis campus of the University of California became an international center of yeast research, and his yeast collection has been utilized by scientists worldwide. I remember well my tasks in Davis, and in Berkeley before that, involving the periodic regrowth on slants of the many cultures in that collection. This important collection of yeast germ plasm containing over 6,000 strains is maintained in Davis by Curator Kyria Boundy-Mills and is known as the Herman J. Phaff Yeast Culture Collection.

Intellectual heritage

Herman was not only an inspiring teacher and friend but also a role model for future academic researchers. He arrived early to work and left late. Because of his example and inspiration, many of his students, coworkers and colleagues near and far were able to achieve international fame for their research. They include, among others, Ahmed T. Abdelal, Don Ahearn, Ed Buecher, Lydia do Carmo-Sousa, Ron Edstrom, Jack Fell, Graham Fleet, Mohamed Foda, Phil Gorin, A. Hagler, Bill Heed, Don Holzschu, Eric Johnson, Elisa Knapp, Andre LaChance, Mike Lewis, Bor-Shiun Luh, Allessandro Martini, Jim Macmillan, Leda Mendonça-Hagler, Marty Miller, Melvin Meyer, Sally Meyer, Demo Pappagianis, Denish Patel, Chet Price, Frank Rombouts, El Tabey Shehata, Moshe Shifrine, Harry Snyder, Masumi Soneda, Frank Spencer, Tom Starmer, Hirosato Tanaka, Tomas G. Villa, R. Whelton, and Minoru Yoneyama. His technicians, Ellen Barker, Gayle Fuson, Mary Miranda, Heather Presley and Joanne Tredick, were well appreciated by Herman and they learned much from this great researcher and teacher.

Herman had an illustrious career of over six decades during which he forged a new science of yeast biology in the interactive fields of systematics, ecology, physiology and biochemistry. Up until the end, Herman continued to be dedicated to studying yeast biodiversity, modernizing his vast collection and making it available to the world. He, his students, and coworkers described over 50 species of yeast in over 300 publications. He was a Charter Member of the American Academy of Microbiology, represented the USA on the International Commission on Yeasts, and was a longtime Editor of the International Journal of Systematic Bacteriology. He also received many honors during and after his lifetime, from the Mycological Society of America, the American Society for Microbiology (J. Roger Porter Award), the US Federation for Culture Collections, the American Society for Enology and Viticulture, the International Commission on Yeast and Yeast-like Organisms, North Carolina State University (John L. Etchells Memorial Lectureship Award), and UC-Davis (Award of Distinction). He was the Editor of the Yeast Newsletter for over 30 years. This publication was a major mechanism for bringing together yeast investigators from all over the world and became the official organ of the International Commission on Yeasts and Yeast-like Organisms of the International Union of Microbiological Societies. A memorable Phaff Symposium took place at the 5th

International Symposium of Yeasts in London, Canada, in 1980. Six years later, Herman was given the honor of presenting his autobiography as the prefatory chapter of the Annual Reviews of Microbiology. Of course, he called it "My Life with Yeasts". In 1996, a special issue of the Journal of Industrial Microbiology was dedicated to Herman in which he contributed the paper "Life with Yeasts during Retirement".

Marinka, Herman's wonderful wife for 37 years, was a major supportive force for him until her death in 1985. Herman's second wife, Diane, was his constant companion until he passed away at the age of 88. Since she was also a musician, she was able to actively share in his love of music.

Herman was an accomplished cellist, a founding member of and performer with the UC-Davis Symphony Orchestra and the Davis Comic Opera Company. He also played in many chamber music groups and was an Honorary Member of the UC Davis Department of Music.

After retiring as Emeritus Professor at UC Davis in 1983, he continued to spend time in the laboratory, collect yeasts in nature, and write until his accidental death in 2001. He loved his work, and had no reason or interest in stopping. We who were the beneficiaries of this man's scholarship, teaching, professionalism and, above all, his deep friendship, owe the success of our careers to Herman Jan Phaff. He taught us how to work hard, be professional, ethical, and, above all, to enjoy our chosen careers!

I will close now with my personal thoughts of Herman on the occasion of his memorial service in Davis on October 29, 2001:

Dear Herman, although I am not a religious man, I believe that you are up there and can receive this message. We met in 1950, not long after I had arrived in Berkeley, a Brooklyn boy without any particular enthusiasm for science. I had been sent to Emil Mrak by Jack Etchells with the goal of making me a food microbiologist. Jody and I drove to California for the first time, and you and I met shortly thereafter. From the beginning, our discussions set me thinking, and I began to appreciate the richness of the scientific life. The excitement that you generated within me as your second student still lives on 51 years later! Like you, I cannot wait to get to the lab in the morning and I drag myself home late in the day. I will never forget our many evenings together in the lab after we had gone home for dinner and then returned for many hours of research and discussion. But I also remember those wonderful parties in your home during which everyone could leave their work behind and simply have fun. You were not only my Professor, but also my dearest friend, my role model and my most important mentor. I will also never forget all those years that we roomed together at the ASM meetings, how we practiced our presentations in front of one another, and all the fun we had at dinners and with our colleagues. You have greatly inspired me, and any heights that I have

reached in science are due to your teaching, your example, and your love. Whenever I will feel in the future that I need a lift, some inspiration, I shall look up at the heavens above and think of you. You were a great scientist, human being and friend, and you will continue to inspire me for as long as I live.

Acknowledgements I acknowledge the following colleagues for their written statements and publications about Herman Jan Phaff from which I 'borrowed' some of the above information: D.G. Ahearn, K.-T. Chung, E.E. Conn, J.W. Fell, G.H. Fleet, C.P. Kurtzman, M.A. Lachance, S.A. Meyer, M.W. Miller and especially H.J. Phaff himself.

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