Hermann Rahn

July 5, 1912 — June 23, 1990

By John Pappenheimer

> I do not wish to be a professor and just sit and count the veins of a butterfly (wing) and then try to determine their names. I could not stand that for long. I am more interested in the whole animal world. . . . My ideal is not a professor but a man like Ernest Thomson Seton. . . by reading his books I try to learn how to live in the woods, how one can sleep warm there in the winter at below freezing temperatures, what wood burns best, how to make a fire in the rain, what provisions one takes on a long trip when you are all alone.

SO WROTE THE SIXTEEN-YEAR-OLD Hermann Rahn to his closest friend and schoolmate, Wolf Tischler, in Germany. Despite these youthful sentiments, Hermann did become a professor and one of the foremost physiologists of his generation. Only a few years later, while still a student, he again wrote to his friend, Wolf, this time saying:

Natural History is not the problem of today, it is merely a good and interesting basis. I believe that experimental zoology with its "cause and effects" has gotten hold of me. . . . I was torn between two worlds. Both afford interesting problems, but I never found a connection between them. You work either systemically and anatomically or on the other hand as physiologist and experimental zoologist. According to my mind the latter offers the greater problems. . . . After being torn between these two worlds it is a good feeling at last to know my way.

These were serious thoughts for a schoolboy, and they reveal Hermann's commitment to research in biology at an early age. In the end he found the connection between the two worlds, and indeed his abiding love of natural history and the call of the wild determined the course of much of his experimental work on respiratory and comparative physiology.

Hermann was brought up in an academic milieu. His father, Otto Rahn, was professor of bacteriology and dairy chemistry, first at Kiel in Germany and later at Cornell University in Ithaca, New York. His mother (neé Bell Farrand, 1883) was a fourth-generation native of Lansing, Michigan, and she was Otto's research assistant at the Agricultural College in Lansing prior to their marriage. Hermann was the eldest of their four children, and most of his formative years were spent in a happy, stable, and intellectually stimulating family environment in Kiel, Germany, and Ithaca, New York. Nevertheless, the first few years of his life were unusually turbulent; no account of his life would be complete without providing brief biographies of his parents and the history of their early married life.

Otto Rahn was one of eleven children born to uneducated Mennonite parents in the little town of Tiegenshof in East Prussia. He was a star student at the town school, and, with the sympathetic support of his father and his mathematics teacher, he was able to attend the University of Göttingen, where he studied physical chemistry with W. Nernst and organic chemistry with Professor Wallach (later to become Nobel laureate in chemistry).

Otto obtained his Ph.D. in 1902 at the age of twenty-one, but academic positions in chemistry were scarce, and he accepted a position in the Department of Dairy Science. His advanced training in organic chemistry and mathematics was unusual in this field, and he soon found applications to bacterial metabolism that brought him international renown. In 1906 he was offered a faculty position in bacteriology at Michigan State and 1907 found him struggling with the English language while teaching chemistry and bacteriology to students in the agricultural college at Lansing.

In the same year, Bell Farrand (Hermann's mother-to-be) graduated from Michigan State and accepted a job as assistant to Professor Clinton Dewitt Smith, who was about to become president of a small agricultural college in Perchicaba, Brazil, six-hours travel west of San Paulo. That was an extraordinary adventure for a well-brought-up young lady from Michigan in 1907, but in her own words, "My nature has always been a bit on the romantic side and having a young and adventurous heart I just could not turn down such an offer to see the world, even though I did not like Mr. Smith." Her romantic nature was to be transmitted and amplified in her son Hermann, whose interests in environmental and comparative physiology led him to roam the world. Bell returned to Lansing in 1908 to join the Department of Bacteriology under Professor Marshall, but she was soon assigned to Otto Rahn as a research and teaching assistant. They were married in 1911, and Hermann was born on July 5, 1912.

Two years later the Rahns boarded a ship for Germany so that Bell could meet Otto's family and show off their two-year-old Hermann to relatives. The Archduke Ferdinand was assassinated while they were on the high seas, and World War I began shortly after they disembarked in Hamburg.

Although Otto was in the process of becoming a U.S. citizen, he and his American bride were classified in Germany as German citizens, and they were not permitted to return to the United States even though Bell was six months pregnant and anxious to return home. Hermann's sister, Marie, was born in November 1914, and soon thereafter Otto was drafted into the army and assigned menial administrative jobs at a small airfield in Latvia.

One of Otto's sisters owned a bookstore in Danzig, and Bell, Hermann, and the baby moved into a room over the store. For the next four years Bell was cut off from communication with her own family in Michigan, and it was not until November 1918 that she learned through the Norwegian Red Cross of her mother's death. Hermann, by then six years old, had no shoes and froze his toes while waiting in line for the daily family ration of 1 pint of skimmed milk. Bell's footwear was reduced to her satin wedding slippers until Otto managed to provide her with a pair of second-hand army boots he had traded for his tobacco rations.

After the war anti-German feelings remained high in the United States, and since Otto had served in the German army he was not invited to return to Michigan. At the same time, German universities were in disarray, and it was not until 1920 that he obtained a suitable post as professor of dairy physics at Kiel. Hermann was then eight years old, and so his early schooling began in Germany. At this time, also, he and his friend Tischler (later to become professor of ecology at Kiel) began collecting and identifying butterflies, insects, birds, and fauna from the beaches of the Baltic Sea. In 1923 his parents were able to transfer Hermann's savings account of $19.00 from America to Kiel, where inflation was such that they were able to buy him a microscope and a camera, "hoping he would someday become a scientist."

In 1925 W. A. Noyes, professor of chemistry at Illinois (and a member of the National Academy of Sciences), made a goodwill tour of German universities, and he became interested in Otto Rahn's work on the physical properties of milk products, noting that no comparable department of dairy physics existed in the United States. Unbeknownst to her husband, Mrs. (Bell) Rahn confided to Noyes that she yearned to return home to visit her family and asked whether it might be possible for him to arrange a lecture tour for her husband. This idea bore fruit, and in 1926 the entire Rahn family visited America, the children learning English from their American cousins while Professor Rahn went coast to coast on his lecture tour. Shortly after returning to Kiel he received an offer to come to Cornell University as tenured professor of bacteriology and dairy physics. Hermann was enrolled in the local high school in Ithaca and started his transition to the American educational system and way of life. The wilderness of the Finger Lake district of upper New York state was in contrast to the manicured country around Kiel, and Hermann was fascinated by it. Throughout his school and undergraduate years at Cornell he spent many days and sometimes weeks camping out in the wilds, collecting or identifying the flora and fauna. During the summers he took jobs as nature counselor at a Boy Scout camp or as assistant in government fisheries or wildlife departments. At college he grounded himself in the chemical and physical sciences needed for his planned career in experimental zoology. After graduating from Cornell in 1933, Hermann returned to Kiel for one year before enrolling as a graduate student and teaching assistant in zoology at the University of Rochester. His roots in Germany were deep, and he was torn between Germany and the United States. It was not until 1936, after a second visit to Kiel, that he was able to write to his friend Wolf, ". . . America has at last become my real home."

CONTRIBUTIONS TO REPRODUCTIVE PHYSIOLOGY OF SNAKES AND BIRDS, 1937-43

Hermann's first publications, based on his independent work as a graduate student, were concerned with the reproductive physiology of viviparous snakes and on the development of the pituitary gland in birds. His discovery in 1937 that viviparous snakes develop a primitive placenta analogous to the mammalian organ won him a National Research Council postdoctoral fellowship to work in reproductive physiology with Frederick Hisaw at the Harvard Biological Laboratories. His year at Harvard (1938-39) was evidently a productive one for it led to a series of eight papers on the structure and function of the pituitary in birds and snakes. With Louis Kleinholz he developed a biological assay for the melanophore-stimulating hormone ("intermedin") of the pars intermedia and determined its activity in a variety of mammalian species. At the same time, he completed a detailed histological study of cell types in the pars anterior of eighteen species of birds and showed that all these species lacked an intermediate lobe. In the same year he found that female garter snakes, collected from Penekese Island off Cape Cod, could store viable sperm in utero for at least one month following insemination, so that the exact time of fertilization of ova and the gestation period were indeterminate. Finally, he found time to court and marry Katherine (Kay) Wilson, a student at the Graduate School of Landscape Architecture.

In September 1939 Hermann moved to his first academic post as instructor in zoology at the University of Wyoming at Laramie. There he made good use of the mountains and prairies to combine his love of nature and natural history with his interests in the reproductive behavior of reptiles. He found that rattlesnakes living at an altitude of 6,000 feet, where the summers are short, have a two-year reproductive cycle, a phenomenon made possible by storage of viable sperm over the winter in a special pocket of the uterus. During the winter hibernation period, also, mature ova were retained in the ovaries and not discharged to meet the sperm until spring. This bizarre schedule meant that at any one time during the summer approximately 50 percent of the adult females were gravid. At lower altitudes, where the summers are longer and warmer, the same species of rattler has a one-year reproductive cycle, and almost all the adult females are gravid. Rahn's principal paper describing this work (published in *Copeia*, 1942) is as convincing as it is interesting, and the simple but original style of this early publication foreshadowed the elegant simplicity of exposition for which he later became noted. His sojourns on the prairies also led him to study reproductive behavior and sexual dimorphism of the sage grouse; when Hermann spoke of the elaborate courtship dances of these birds, you listened to sheer poetry.

PULMONARY MECHANICS AND BLOOD-GAS EXCHANGE; YEARS WITH WALLACE FENN, 1941-56

World War II and chance events abruptly altered the course of Rahn's career and the direction of his research. Of the chance events, undoubtedly the most important was his meeting with Wallace Fenn in Rochester in the summer of 1941. This meeting occurred when Hermann, coming east from Wyoming for a visit to his parents, stopped briefly in Rochester to visit friends before proceeding to Ithaca. He called on Fenn, whom he greatly admired, and before their conversation was over Fenn offered him a job as instructor in physiology, an offer that was accepted on the spot. Fenn was already one of the most distinguished general physiologists in the country, having made pioneer contributions to the mechanism of phagocytosis, the heat production of contracting muscle, the metabolism of active nerve, and the exchange of electrolytes in excitable tissues.[1] Hermann was to become Fenn's closest colleague, confidant, and scientific protégé. Shortly after the United States entered World War II, the National Research Council asked Fenn to investigate the possibility that the operational altitude of Air Force personnel might be increased by breathing oxygen under pressure (positive pressure breathing). Neither Fenn nor his junior colleagues had ever worked in the field of human respiration, but they accepted the challenge and in the period 1941-45 developed fundamental new approaches to pulmonary mechanics and respiratory gas exchange--concepts that helped to introduce a golden age of theoretical and applied respiratory physiology in the decade following World War II. In this development, Hermann Rahn played a central role, although his association with Fenn and other colleagues was so close that it is difficult for a biographer to separate the relative contributions made by each individual. It is reasonable to suppose, however, that Fenn's quantitative biophysical approach awakened latent talents in Hermann Rahn that made him a full partner in the enterprise and shaped his own approach to biological problems during the next forty years.

Two major contributions to respiratory physiology emerged from the 1941-45 work on positive pressure breathing by the Rochester team, and both were published in 1946 in the *American Journal of Physiology*. The first was titled "The Pressure-Volume Diagram of the Thorax and Lung" with Rahn as senior author; the second was "A Theoretical Study of the Composition of Alveolar Air at Altitude" with Fenn as senior author. The first paper became the starting point for research on pulmonary mechanics in many physiological and clinical laboratories. The second paper provided a graphical solution to equations describing the partial pressures of oxygen and carbon dioxide in alveolar gas as a function of barometric pressure (altitude), inspired gas composition, and respiratory exchange ratio. While most of the equations underlying this analysis had been derived independently by others, their representation in a graphical form that could easily be understood and applied to a variety of problems was a major contribution comparable to the classic nomographic analysis of blood chemistry by L. J. Henderson.[2] Indeed, the next important step was to extend the analysis to the blood-gas exchange, and in 1949 Rahn published his now classic paper titled "A Concept of Mean Alveolar Air and the Ventilation-Blood Flow Relationships During Pulmonary Gas Exchange." In this paper Rahn showed how regional differences in the ratio of alveolar ventilation to alveolar blood perfusion (V_A/Q) give rise to oxygen pressure differences between mean alveolar gas and blood leaving the lungs. His analysis was presented in a clear graphical form that has been used by many subsequent investigators. At the time of this work, there were no experimental methods for determining regional pulmonary blood flow or ventilation, and Rahn had to assume normal Gaussian distributions in order to provide numerical solutions in graphical form. More than ten years later, when methods for determining regional ventilation and perfusion using radioactive gases had been developed by J. B. West[3] and others, it was found that the distribution of V_A/Q was far from Gaussian. Nevertheless, the new experimental data were easily incorporated into Rahn's theoretical analysis, which continues to be the preferred means of presenting the data. Abnormalities of V_A/Q, rather than diffusion capacity, proved to be the most common cause of poor oxygenation of arterial blood in a variety of pulmonary diseases, and Rahn's analysis provides the theoretical basis for clinical tests of impaired gas exchange.

The techniques and concepts developed to investigate respiratory gas exchange during acute exposure to low barometric pressures (altitude) were well suited to studies of other perturbations of the respiratory environment, including the inhalation of CO_2, hyperventilation, breath-holding, diving, and acclimatization to altitude. All of these perturbations were studied by the Rochester team, but for Rahn the lure of the mountains was not to be denied, and during the immediate postwar years he organized three expeditions to high altitudes in Wyoming, Colorado, and the Peruvian Andes. He and his colleagues were first to show that respiratory acclimatization and deacclimatization to altitude, measured in terms of alveolar gas composition, occurs exponentially with a half-time of about twelve hours. The results were clearly delineated as a hysteresis loop on the Fenn-Rahn O_2-CO_2 diagram, and they provided the starting point for subsequent studies by Severinghaus[4] and others showing that the time course of acclimatization is determined by changes in composition of cerebral fluids bathing medullary chemoreceptors.

BLOOD-GAS EXCHANGE AT HIGH AND LOW PRESSURES; PHYSIOLOGY OF DIVING IN THE AMA (DIVING WOMEN) OF KOREA AND JAPAN, 1956-68

In 1956 Rahn moved to the University of Buffalo Medical School as chairman of the Department of Physiology and with him moved the center of gravity of the Rochester school of respiratory physiology. In the years to come he was to attract more than 100 collaborators from some twelve countries to work on such diverse topics as respiratory gas exchange in diving insects, the regulation of pH in poikilotherms, the role of nitrogen in the absorption of gas pockets in animals and humans, distribution of ventilation and perfusion in health and disease, respiratory gas equations as applied to gill breathing, the physiology of diving in the Ama sea-women of Korea and Japan, and allometric studies of gas exchange through the eggshells of developing bird embryos ranging from hummingbirds to ostriches. Although each of these topics was interesting in itself, Rahn always sought for generalities and for ways to present both the problem and its solution so clearly that even a nonspecialist could appreciate its interest and significance. For this reason he was invited to give many public lectures, and the following examples taken from the titles of some of his lectures or essays will illustrate the point:

- The Unique Behavior of Nitrogen Gas
- Breath Holding in the Mountains and Underwater
- Lung Collapse and Our Space Missions
- Hydrogen Ion Regulation, Temperature, and Evolution
- The Diving Women of Korea and Japan
- How We Store Oxygen
- Why Fish Have Very Low Arterial CO_2 Tensions
- How Eggs Breathe

Rahn's interest in the physiology of diving arose from his analysis of gas exchange during breathholding, and eventually this led him to investigate the remarkable diving ability of the diving women of Korea and Japan. This work was catalyzed by S. K. Hong, a Korean physiologist who came to Buffalo to study respiratory physiology with Rahn. Together they organized expeditions to the coasts and islands of southern Korea and Japan, where for centuries women divers have harvested the sea floor for food, using only face masks for equipment and enduring high pressures and extreme cold. Using a simple but ingenious device for collecting alveolar samples underwater, Rahn and Hong were able to chart the changes of alveolar gas composition as a function of time and pressure during dives by specially trained native divers. Compression of the lungs during dives to 7 to 10 meters produced correspondingly increased gas pressures, but, of course, oxygen was consumed, so expansion of gases during ascent to the surface caused rapid decrease of oxygen pressure to astonishingly low values--so low in fact that blood entering the lungs lost oxygen to the gas phase and imperilled consciousness. Detailed quantitative explanation of this reversal and the critical conditions for surviving free dives were subsequently worked out in the home laboratories in Buffalo and Seoul, and in subsequent years, also, the physiological adaptations of these hardy women to extreme cold were investigated. A popular account of this work was presented by Rahn and Hong in a *Scientific American* article (1967). Several of the young Korean medical doctors enlisted to help with this project were stimulated to choose physiology as a career, and indeed this collaborative enterprise introduced modern respiratory physiology to both Korea and Japan. This was a special satisfaction to Rahn, who was awarded an honorary LL.D. degree from Yonsei University in 1965. At this stage of his scientific career, Rahn's important contributions to respiratory physiology were also recognized by his election to the American Academy of Arts and Sciences, the presidency of the American Physiological Society, and in 1968 to the National Academy of Sciences.

GAS EXCHANGE IN AVIAN EGGS AND ITS ROLE IN EMBRYONIC DEVELOPMENT, 1968-90

In 1968 Rahn started a completely new venture, namely the respiratory physiology of avian eggs and embryos. This project was to be the principal focus of his research until his death in 1990 and to it he brought an unprecedented knowledge of respiratory gas exchange combined with his lifelong enthusiasm for field studies in classical zoology. In the preface to his two-volume collection of papers in this field he remarks, "The beginning of our interest in gas exchange of avian eggs can be clearly documented. It occurred in 1968 after the arrival of Douglas Wangensteen as a Postdoctoral Fellow. . . . One day he asked us how eggs breathe. Since none of us had even thought about this problem, we suggested that he might find out." Wangensteen and Rahn soon determined that exchange of oxygen, CO_2, and water vapor occurs principally by simple passive diffusion through pores in the shell, and this raised a host of basic questions. If gas exchange is limited by diffusion through the shell, how do gas pressures in the tissues change as the embryo increases in size and metabolism during incubation? What determines the number, diameter, length, and total area of the pores in the shell? How are pore dimensions adjusted to provide sufficient conductance for respiratory gases but without fatal loss of water vapor? What are the relations between pore area, thickness of shell, and gas conductance as a function of egg sizes from 1 gram (wrens) to 1,500 grams (ostriches)? How does porosity of eggs at high altitude compare with those of the same size at sea level? Can birds from sea level adjust the porosity of their eggs to compensate for changed diffusivity and oxygen pressures at altitude? The answers to almost all these questions and many more were described in some seventy publications with more than fifty collaborators from around the world. The answers involved measurements of gas exchange on fresh fertile eggs from some 100 species of birds nesting in locations from Spitsbergen to remote islands of the South Pacific, from the deserts of Israel to the Himalayas, from Alaska to the nesting mounds of wild turkeys in Australia. Two illustrations (Figures 1 and 2) from a *Scientific American* article titled "How Birds Breathe" by Rahn, Ar, and Paganelli (1979) are reproduced in this memoir because they exemplify the generality of Rahn's thinking and the elegant simplicity of his expository skill. Rahn's last paper, published posthumously, was on a noninvasive recording of the heartbeat of developing bird embryos by means of a microphone placed in a sealed chamber containing the egg.

SERVICE TO SCIENCE: NATIONAL AND INTERNATIONAL

Rahn was a member of numerous scientific societies, and he received distinguished service awards from several of them. However, his primary allegiance was to the American Physiological Society (APS) and to the International Union of Physiological Sciences (IUPS). He was president of APS (1963-64) and served for many years as scientific editor and board member of its publications, including the comprehensive and scholarly two-volume *Handbook of Respiratory Physiology*, which crowned more than a decade of major advances in this field. He also gave generously of his time to advisory panels of the National Research Council, the National Institutes of Health, the National Aeronautics and Space Administration, and the American Institute of Biological Sciences.

Travel and international aspects of physiology played a major role in Rahn's life. His roots in Europe, his collaborative research with physiologists from many countries, and his sensitivity to different cultures gave him a strong voice in the International Union of Physiological Sciences. He served on its council from 1965 to 1971 and subsequently as its vice-president. From Wallace Fenn he absorbed a strong tradition of loyalty to the triennial international congresses of physiology, and he served on the executive committee of the large and successful XXIVth Congress held in Washington, D.C., in 1968. On several occasions he served as resident visiting professor at foreign universities.

TEACHER, SCHOLAR, AND GENTLEMAN

Rahn grew up in a prewar academic environment in which research was regarded as a joyous, spare-time privilege of a university teacher rather than a driving professional career. This point of view changed rapidly after the war, when large-scale government support for research made it possible for young scientists to create individual research empires without regard for teaching or other traditional academic responsibilities. Rahn was especially vulnerable to this development because his research on gas exchange at high and low barometric pressures had important applications to both clinical and military problems. He was well supported by contracts from the Air Force and the Office of Naval Research as well as from the National Science Foundation and the National Institutes of Health; it would have been easy for him to neglect his teaching and university responsibilities, but to this temptation he never succumbed. Instead, he remained true to his principles, namely, that the primary responsibility of university professors is to their students and departments. At the time he moved to Buffalo in 1956, he organized a comprehensive course in human physiology for medical students, and he continued to play a major role in teaching it throughout his tenure as head of the department. At the same time, he created a stimulating research environment for all members of his staff as well as for the continual stream of postdoctoral fellows, many from abroad, who came to work with him. He was a magnetic source of ideas, drawing in all those around him, and over the years he collaborated and published with all fourteen of his permanent staff members. As one staff member put it, "[Rahn] had a way of sharing his excitement over a new idea and before you knew it both of you were in the lab trying it out."

Hermann Rahn was equally at home in the wilderness and in the most formal settings. In civilized society he usually dressed impeccably, and his innate courtesy, modesty, and sensitivity to others (perhaps best described as "courtliness") allowed him to fit in with all social situations, however foreign or sophisticated. His concern for others and his willingness to take on responsibility endeared him to all those who had the privilege of working with him. I have a vivid memory of an exhausted Hermann after he hosted a three-day meeting of 800 members of the American Physiological Society in Buffalo; he was walking back to the lab with drooping shoulders, laden with shopping bags full of presents for the secretaries and others who had helped him organize the meeting.

In 1973 Rahn retired as chairman of the department and became distinguished service professor of physiology. The international renown he brought to this university was further recognized by various awards, including the Stockton Kimball Award in 1969 and the Chancellor Norton Medal in 1981. In 1985 the experimental diving laboratory that had been constructed by the Office of Naval Research for Rahn's studies of underwater physiology was renamed "The Hermann Rahn Laboratory of Environmental Physiology."

In the spring of 1990 Rahn learned that he had incurable pancreatic cancer, but he continued to work in the lab as long as physically possible, and he was working on a manuscript in bed at home a few days before the end. In one of his last letters to his lifelong friend Wolf Tischler he commented on his life:

> . . . the general maturing of a happy child with his insect collecting, his love with all nature, his wonders and aspirations . . . to the mature student, the young investigator and finally the reflecting scientist . . . I am happy to have stayed a *romantic* in science. Today my colleagues have become *business* scientists and I am sure your colleagues have to do the same in order to survive as researchers. So we have both been most fortunate because we are both in a sense still children, with our youthful enthusiasm to explore and search for answers.

ACKNOWLEDGMENTS ARE DUE PROFESSOR Wolfgang Tischler for reading the manuscript of this memoir and for giving permission to quote from his correspondence with Hermann; Hermann's sister, Marie Wohlmann, and his son, Robert, for allowing me to read and quote from the typewritten autobiographies left to them by Otto and Bell Rahn; and members of Rahn's staff at Buffalo, especially Charles Paganelli, R. Blake Reeves, and Augusta Dustan for their comments.

NOTES

1 See "Wallace O. Fenn," in *Biographical Memoirs*, vol. 50, pp. 141-73. Washington, D.C.: National Academy of Sciences, 1979.

[2] L. J. Henderson. *Blood: A Study in General Physiology*. New Haven, Conn.: Yale University Press, 1928.

[3] J. B. West. *British Medical Bulletin*, 19(1963):53-60.

[4] J. W. Severinghaus, et al. *Journal of Applied Physiology*, 18(1963):1155-56.

SELECTED AWARDS AND DISTINCTIONS

1938-39

National Research Council fellow

1960

Harvey Society lecturer

1963-64

President, American Physiological Society

1964

Doctor of medicine, Honoris Causa, University of Paris

1965

Honorary LL.D., Yonsei University, Seoul

1966

American Academy of Arts and Sciences

1968

National Academy of Sciences

1971

Institute of Medicine

1971-74

Vice-president, International Union of Physiological Sciences

1973

Albert Behnke Award, Undersea Medical Society

Honorary D.Sc., University of Rochester

Distinguished professor, State University of New York at Buffalo

1976-77

Alexander von Humboldt Award and visiting professor, University of Göttingen

1977

Painton Award, Cooper Ornithological Society

1980

Profesor honorario, Universidad Peruana, Lima

1981

Doctor of medicine, Honoris Causa, University of Berne

1981

Elliott Coues Award, American Ornithological Union

Chancellor Norton Medal, State University of New York at Buffalo

1985

Dedication of the Hermann Rahn Laboratory for Environmental Physiology, State University of New York at Buffalo

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1953

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