NATIONAL ACADEMY OF SCIENCES

WALLACE OSGOOD FENN

1893—1971

A Biographical Memoir by
HERMANN RAHN

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W. O. Fenn

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August 27, 1893–September 20, 1971

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WALLACE OSGOOD FENN was born in Lanesboro (Berkshire County), Massachusetts and died in Rochester, New York in his seventy-ninth year, after a brief illness. He is survived by his widow, Clara Bryce (Comstock) Fenn; his children, William Wallace Fenn, Ruth (Fenn) Starman, Priscilla (Fenn) Roslansky, and David Bryce Fenn; and ten grandchildren. He led a most vigorous life and up to his very last days was working in the laboratory; during his last three years he shaped the new directions of the International Union of Physiological Sciences as its President. To many of his colleagues he was the Dean of Physiological Sciences, the last Renaissance Man, whose basic contributions covered so many areas and who had a remarkable perspective on the whole field of biology.

His forefathers settled in New England in the seventeenth century. William Wallace Fenn, his father, was a Unitarian minister who had married Faith Huntington Fisher, also from New England. Later his father became the Bussey Professor of Theology at Harvard and Dean of the Divinity School. Thus Wallace Fenn's childhood was spent in Cambridge, where he attended the Cambridge Latin School and entered Harvard with the goal of preparing himself for the ministry. However, when he started cutting his father's lectures to attend plant physiologist W. J. V. Osterhout's classes in biology, the foundations were laid for a career in physiology that was to span more than half a century.

Fenn graduated in 1914. His graduate work at Harvard with Osterhout was interrupted by World War I, during which he served in the Sanitary Corps of the U.S. Army and was commissioned a Second Lieutenant. Upon discharge in 1919, he finished his doctoral thesis in June, married Clara Bryce Comstock in September, and began his appointment as an Instructor in Applied Physiology in the Department of Industrial Hygiene at the Harvard Medical School under Cecil K. Drinker. Here began his classical studies of phagocytosis of solid particles by white blood corpuscles.

In 1922 he accepted a Rockefeller Travel Fellowship and was the first American to work in A. V. Hill's laboratory in London, England. This was followed by a six-month stay in H. H. Dale's laboratory at the National Institute for Medical Research in London. Returning to this country in 1924, he accepted the Chair of Physiology at the newly formed Medical School at the University of Rochester, New York. This position he filled for thirty-five years. In 1961 he was named Distinguished Professor of Physiology, a post he occupied until his death in 1971.

THE SCIENTIST

Fenn's first paper was published in 1916 in the *Proceedings of the National Academy of Sciences*. It was entitled "Salt Antagonism in Gelatin." His last paper, "Partial Pressure of Gases Dissolved at Great Depth," was published posthumously in *Science* in 1972. During the intervening half-century his 267 publications can be conveniently divided into four general areas: the physiology of muscle, electrolytes, respiration, and high pressure. In each area he laid foundations of new concepts, and when he was satisfied that he had made new basic contributions, moved on to explore new fields.

CONTRIBUTIONS TO MUSCLE AND ELECTROLYTE PHYSIOLOGY

The work that brought Fenn his first recognition was his study on the heat production of muscle, which he started in A. V. Hill's laboratory in 1922–1923. Fenn wrote: "In particular it can now be shown that there is a fairly good quantitative relation between the heat production of muscles and the work which they perform, and that a muscle which does work liberates, *ipso facto*, an extra supply of energy which does not appear in an isometric contraction."* It was A. V. Hill who referred to this as the Fenn Effect, and so it has been known ever since.

Fenn's heat data showed first of all that if a muscle shortens, no matter how little and no matter how lightly loaded, it produces more heat than during an isometric contraction over the same time period. He then showed that this extra heat production was proportional to the external work done by the muscle. It was clearly not determined by the load alone, nor by the change in length. This was the first evidence, and remains today the best evidence, that shortening is an active process and that muscle is not simply a prestretched spring shortening passively. The Fenn Effect has emerged as the nearest thing to a law that muscle physiologists have.

Following his pioneer work on muscle heat production, Fenn began to measure gas exchange by nerve and by muscle. To this end he had to invent a number of ingenious instruments to obtain the necessary specificity and precision. In 1927 he measured for the first time the quantitative amount of oxygen required by a nerve to conduct an impulse. Similar studies on the metabolism of contracting muscles led him to consider the role of electrolytes, particularly potassium, in nerve and muscle

*Wallace Osgood Fenn, "A Quantitative Comparison between the Energy Liberated and the Work Performed by the Isolated Sartorius Muscle of the Frog," *Journal of Physiology*, 58(1924):175.

activity. At the time, although it was known that muscle fibers were rich in potassium, almost nothing was known of the mechanisms by which cells accumulated and maintained a high potassium content.

The work ushered in the era of electrolyte physiology. Beginning in 1933 Fenn virtually created the field of potassium metabolism. He made the first determinations of potassium, sodium, magnesium, and calcium in nerve. He developed a new method for determining internal pH of muscle and nerve and obtained values that remain acceptable today. He showed that intracellular potassium was mobile, not fixed, and that muscle potassium shifted in response to various environmental factors.

Most importantly, he showed that during contraction potassium was lost from muscle in exchange for sodium, and that the process was reversed in recovery. For the first time he showed that sodium could penetrate muscle. These observations were clearly the necessary foundation for the Hodgkin-Huxley hypotheses concerning initiation and propagation of nerve and muscle impulses and the magnitude and polarity of electrical potential differences across cell membranes. As early as 1936, at the Cold Spring Harbor Symposium, Fenn said, "The explanation of a loss of potassium from a muscle during activity is a matter of fundamental theoretical importance. In terms of the theory which I have been using as a guide, it is interpreted as an increase in the permeability of the muscle membrane of sufficient extent to permit sodium, but not chloride, to enter. Every molecule of sodium which enters then displaces one molecule of potassium."*

Fenn showed that potassium escaped from muscle during contraction *in situ* and that a large part of this potassium appeared in the liver. He demonstrated that potassium uptake was

*Wallace Osgood Fenn, "Electrolytes in Muscle," *Cold Spring Harbor Symp. Quant. Biol.*, 4(1936):252–59.

linked with carbohydrate metabolism, particularly with glycogen deposition, and developed the concept that potassium tends to follow the Cori cycle. He was always quick to seize new opportunities. When radioactive potassium became available to him in 1939, he ingested a sample. Using himself as subject, he was thus the first not only to study the kinetics of potassium metabolism but also to demonstrate potassium incorporation into blood cells, previously thought to be impermeable. He showed that nearly all muscle potassium in the body is exchangeable, proving that high intracellular potassium content is not maintained by binding or sequestration of potassium, an idea which was consonant with his notion that potassium is maintained by an active energetic process.

CONTRIBUTIONS TO RESPIRATION PHYSIOLOGY

The entrance of Wallace O. Fenn into the history of respiratory physiology can be precisely dated. It was within days after the U.S. entry into World War II. At that time he was forty-eight years old and had established himself as the acknowledged leader in the physiology of muscle and electrolytes. He was to be recognized in 1943 by election to the National Academy of Sciences.

Wallace Fenn was drawn into respiratory physiology by his desire to contribute to the war effort. This was to be largely a war in the air, and from a military point of view, supremacy in altitude tolerance meant supremacy of air power. The airplanes of that day did not yet have pressurized cabins, but the possibility occurred that the human lung might be pressurized by application of positive pressure breathing. The question was whether man's lungs could tolerate a sufficient amount of pressure to raise the partial pressure of oxygen to a significant degree, or would the lungs rupture, or would the circulation stop? What were the limiting factors? What were the hazards?

What was known about respiratory physiology in general? This can best be answered by listing some terms which did not appear in the physiology textbooks of that era, but which are commonplace today. Such terms are: *positive and intermittent pressure breathing, pressure–volume diagram, work of breathing, pulmonary compliance, airway resistance, alveolar gas equation,* O_2-CO_2 *diagram, ventilation–perfusion ratio,* just to name a few.

Wallace Fenn had never worked in the field of human respiration. The equipment in his laboratory would be regarded as primitive by current standards. Among the more useful items were a few assorted spirometers, two or three Haldane machines, an equal number of Van Slykes, and several U-tube manometers. The most sophisticated instrument was a Millikan ear oximeter, which had been loaned to him by the Military. It carried a security classification of a fairly high level, and since no instruction manual came with it, it took some time and a visit to Glen Millikan himself before anyone could figure out how to use it properly.

In addition to this modest inventory of equipment, Fenn had three young instructors, all trained in biology departments. They knew all about such things as how fast the drosophila can beat its wings, how and why the rattlesnake changes color, and how to activate or inhibit enzymes found in grasshopper eggs, but none of them had ever blown a vital capacity; neither did they know the difference between complemental and supplemental air. L. E. Chadwick, A. B. Otis, and H. Rahn, living with their wives on postdoctoral stipends which were only a fraction of what a graduate student receives today, were the most unlikely crew to have been assembled for the unknown job that lay ahead of them.

Neither the equipment nor the staff was very impressive, and it seems doubtful that by present standards the project could have qualified for a National Institutes of Health grant. However, the major asset, recognizable even then, was Wallace Fenn himself. He was not put off by lack of ready-made equipment; he was well endowed with Yankee ingenuity, and he loved to improvise. He could, with whatever components happened to be handy, construct apparatus that would perform in a reliable and effective fashion. Everyone associated with him has memories of him in the laboratory surrounded by what at first sight appeared to be an unrelated jumble of strange wires and rubber bands, tubing, pulleys, lenses, light sources, mirrors, and other assorted bits and pieces. A more careful examination suggested there might be some order in the arrangement, and further observation would reveal that something of physiological interest was actually being measured and perhaps even graphically recorded. A relatively refined example was a device for the automatic recording of blood flow through the finger and its alteration by pressure breathing.

The high-altitude chamber was perhaps the crowning masterpiece of Fenn's ingenuity. He had received from the Committee on Medical Research of the Office of Scientific Research and Development a contract which provided the sum of $500 (five hundred!) for special research equipment. From this budget he bought a steel tank designed for the processing or transport of beer, commandeered the tree-spraying pump from the University Grounds Department, reversed its valves, and connected pump to tank. The result was a chamber which could go to simulated altitudes at the rate of 5,000 feet per minute. As he later said, "It surely was the worst high altitude chamber in the country, but a rare atmosphere is the same wherever you find it."*

Not only could he get the most out of primitive pieces of equipment, but he also seemed somehow able to evoke the best output from his staff. He did not tell people to do things. Rather, he pointed out things that needed doing and waited for some-

*Wallace Osgood Fenn, "Born Fifty Years Too Soon," *Annual Review of Physiology,* 24(1962):1.

thing to happen. He worked hard himself and expected others to do likewise, but he recognized that there were individual differences in effective work patterns and did not try to impose his own habits on others. Although he kept rather regular working hours himself, he apparently was not perturbed by those with more erratic habits. Getting something done rather than compulsive adherence to a fixed schedule was the important thing.

In starting a new experiment he frequently took the lead by setting up apparatus himself rather than asking someone else to do it. Typically, he would insist on being the first subject in a new experimental procedure, and in experiments with pressure breathing and in the altitude chamber he extended himself on a number of occasions to the point of losing consciousness. He was a pioneer in every sense, and it was a blessing that his work antedated the Human Subjects Review Committee.

Fenn's intuitive approach to and logical analysis of the pressure breathing problem led him to develop two powerful concepts and to express them in the form of graphic relationships: the pressure–volume diagram of the lung and thorax, and the O_2-CO_2 diagram of the composition of alveolar gas.

Although the basic pressure–volume (P–V) diagram had been previously developed by F. Rohrer, Fenn conceived it independently, elaborated it further, and distilled into it some ten years of work and thought. Like all his work, it defined physiological boundaries, limiting values for muscle forces and the corresponding volumes of gas and blood. Within these limits were centered the normal operating range of pulmonary mechanics and the response of the system to positive and negative pressure breathing. It was not only a beautiful composition both artistically and scientifically, but it was also the foundation and framework of respiratory mechanics that would be further embellished by students during succeeding decades.

Fenn's second masterpiece, the O_2-CO_2 diagram, did for pulmonary gas exchange what the P–V diagram did for respiratory mechanics. With it he could represent all parameters of the alveolar gas and ventilation equations. He never claimed to have originated these equations, but he derived them independently, made sure they were correct, and put them in graphic form. As somebody put it, "That's when he made them sing." On the diagram he could show all possible compositions of alveolar gas and the arterial blood under any specified set of conditions. He could indicate normal ranges and limits of survival as well as the pathways followed during hyperventilation and asphyxia and during exposure to CO_2, altitude, or hyperbaric pressures. It could be used to demonstrate ranges of normal and impaired performance. It was indeed a theme that could be sung with many variations.

Although the P–V and O_2-CO_2 diagrams represent great masterpieces of Fenn's scientific artistry, he created, inspired, or contributed to many other works. To give a few examples: development of the concept of an optimal breathing frequency, measurement of alveolar pressure, dynamic pressure–volume curves presented for the first time on a cathode ray oscilloscope, development of an infrared CO_2 meter, and probably the first published continuous recording of CO_2 changes during a single breath.

Finally, one must mention two special contributions to respiration physiology, a lasting monument to his effort in this area: his book, *A Graphical Analysis of the Respiratory Gas Exchange,* which went through many reprintings, and his editorship of *Respiration* in the *Handbook of Physiology* series, both of these published by The American Physiological Society.

CONTRIBUTIONS TO THE PHYSIOLOGY OF SPACE AND OCEANS

From the mid-1950s Fenn became greatly intrigued with two new frontiers that began to unfold—man's explorations in space and the ocean depths. While his research continued in very basic experiments, their application was obviously directed to filling in the gaps of knowledge so that man could exist successfully in these new environments. He was in great demand as a consultant by space physiologists and tried to convince his more earth-bound colleagues of the great new opportunities in physiology that unfolded as man ventured into space. Every problem Fenn "considered basic, if the investigator put some basic thinking into it." In that sense he felt that physiology as a science had gained immeasurably and would continue to grow as man went forth in orbit and into the oceans—thoughts that he expressed so well in his address "Physiology in Orbit."*

Wherever man went he needed oxygen as the life-sustaining gas, yet when it exceeded normal pressures it became poisonous. Fenn spent many years with his associates (R. Gerschman and D. L. Gilbert) in trying to understand the toxic nature of oxygen. Probably his most important insight was the recognition and demonstration that oxygen poisoning and X-irradiation effects have the same common mechanism.

He also turned his attention to the effects of high inert gas pressures upon the metabolism of unicellular organisms and the effects of hydraulic pressure on biological reactions. His last benchwork emphasized the importance of partial molar volume concepts as a tool for determining the volume that O_2 occupies within the hemoglobin structure.† His last research concerned itself with the theoretical concepts of partial pressures of gases dissolved at great depths. It was a thermodynamic interpretation published posthumously in *Science*,‡ where with his great modesty he asked for the help of physical chemists to develop this concept in greater detail, help which shortly appeared.§

* Wallace Osgood Fenn, "Physiology in Orbit," *The Physiologist*, 3(1960):20–26.

† Wallace Osgood Fenn, "Partial Molar Volumes of Oxygen and Carbon Monoxide in Blood," *Respiratory Physiology*, 13(1971):129–40.

‡ Wallace Osgood Fenn, "Partial Pressure of Gases Dissolved at Great Depth," *Science*, 176(1972):1011–12.

§ F. C. Andrews, "Gravitational Effects on Concentrations and Partial Pressures in Solutions: A Thermodynamic Analysis," *Science*, 178(1972):1199–1201.

SERVICE TO SOCIETIES

In spite of his active life as benchworker and teacher, few physiologists have given more of their time to professional societies. For twenty years Fenn served in many capacities in the American Physiological Society—as a member of the Board of Publication Trustees, Treasurer and Secretary, and its President (1946–1948). He later took upon himself the difficult task of writing the *History of The American Physiological Society: The Third Quarter Century, 1937–1962* (1963).

He served as President of the American Institute of Biological Sciences (1957–1959); as Chairman of the Advisory Council of the Life Insurance Medical Research Fund; as Chairman of the Physiology Study Section and the Physiology Training Grant Committee of the National Institutes of Health; and as a member on various boards of the National Institutes of Health, the National Academy of Sciences (Chairman, Section of Physiology, 1954–1957; Council 1966–1969), the National Research Council, and the National Science Foundation. But of all organizations, his greatest empathy was directed toward the International Union of Physiological Sciences (IUPS). This he felt was a vehicle that could bring under one roof physiologists from all over the world. For him physiology was the great encompassing science which could bring all men to a common outlook and worldwide understanding. He chaired the U.S.A. National Committee for the International Union of Physiological Sciences from 1946 to 1950, became Secretary General of IUPS (1959–1965), and edited the *History of the International Congresses of Physiological Sciences, 1889–1968*. His American colleagues elected him President of the XXIV International Congress of Physiological Sciences in Washington, D.C. in 1968, and on that occasion, which was his seventy-fifth birthday as well, he was elected President of IUPS for a three-year term, 1969–1971.

The XXV International Congress of Physiological Sciences in Munich, where Fenn was to officiate as President, was for him the crowning point of his lifelong devotion to physiology and a long sought-after personal reward to see thousands of physiologists from all countries assembled in peaceful discussion. Yet this goal eluded him. Shortly before the meeting he was suddenly taken ill and died in his home in Rochester, New York, on September 20, 1971.

A more intimate glimpse of Wallace Fenn's philosophy and attitude about the role of physiology in the world of science can be found in: "Physiology on Horseback," *American Journal of Physiology,* 159(1949):551–555; "Physiology in Orbit," *The Physiologist,* 3(1960):20–26; and "Born Fifty Years Too Soon," *American Review of Physiology,* 24(1962):1–10.

THE MAN AND TEACHER

Reviewing his contributions as a leader and a scientist, one might well imagine a man who unconsciously dominated the scene on the public forum or in his own laboratory. Wallace Fenn was quite the opposite. By nature he was shy, a man who did not seek out his fellow man with a great hello. He kept his own counsel, and for many he was not easily approachable. Once such barriers were broken, he was a most friendly, completely unpretentious person who would listen to your story politely but only respond when necessary. In public forums and committee meetings his patience with conflicting points of view was on occasion wondrous to behold. While others fumed and fussed, he would sit in silence, but when he finally spoke, it usually ended the debate. He was a master in the art of compromise without compromising principles.

Many of his friends and colleagues remember the joyous weekends at the Fenns' summer cottage on Canandaigua Lake. There was always a cooperative program of felling trees, getting boats out, cutting wood, raking the beach, rebuilding the pier, projects in which everyone happily joined. His New England heritage enforced his belief that work came first and then play, and it required real effort for him to sit with idle hands when there was a job to be done or a boat to sail. He had an amazing physical endurance and never took an elevator to his laboratory on the fourth floor. I remember his suggesting after a cafeteria lunch that we run up the four flights while holding our breath. He loved all types of physical and intellectual competition.

He had the knack of getting others to work with him without ever issuing an order. He simply expected people to come forward to help in a common cause, whether it was in teaching, research, or committee meetings. If they failed to do so, he would do the job himself without reprimand. He also had an amazing sense of timing; when a tough decision had to be made, he would wait, always just long enough so that either the problem evaporated or the involved person had solved it for himself, and feelings were never hurt.

Wallace Fenn had a soft spot in his heart for the proverbial underdog. Few people realize how much aid and comfort, protection, and encouragement he gave to those who had tough luck or seemed to have failed in their professional accomplishments. Nothing gave him more pleasure than to see someone fight his way up through temporary odds, real or imagined. All he asked from them was that they show pluck, patience, and perseverance. (Parenthetically, Fenn loved alliteration.)

Teaching he considered a most serious assignment. He was never satisfied with last year's lectures, and year after year tried new and better ways of getting a difficult point across. It was this quality of continuous striving that endeared him to his students and colleagues in lectures and seminars. His lectures to the students were exemplary in their clarity, and yet he was always able to instill the sense of wonder and the new challenges that lay ahead for a better understanding.

Wallace Fenn considered it a great privilege to work as an academician, but felt that this special privilege demanded an utter devotion and enthusiasm, as well as giving help to other colleagues, to his professional societies, and to his government when so called upon. For him continuous striving, striving to obtain his scientific goals, was more important than arriving. He was most embarrassed by the many honors that were bestowed upon him. For him these were not signals that he had arrived. A remarkable inner drive prompted him to continue his strivings, and during his last days, propped up in bed, knowing that the end was at hand, he was slavishly working on his final theoretical manuscript, mainly concerned that he had derived his equations correctly.

Spanning a most productive scientific career of more than half a century, many honors and recognitions (listed below) were bestowed upon him. These were given partly in recognition of the many accomplishments of a scientist whose vision and work had spanned so many areas in physiology and in part to honor a man who had given so much of himself that physiology as an encompassing science had become a greater science in the world.

A most unusual award was the dedication of the "Respiration Suite" to Wallace Fenn. It was composed by Jurriaan Andriessen and performed by the Dutch Wind Ensemble at Alphen, Holland, in the presence of several hundred physiologists and our Ambassador, to honor the man who had contributed so much to the physiology of the lung, which is also a device for the creating of harmonious sounds.* In 1968 a Jubilee Issue in his honor, on the occasion of his seventy-fifth birthday, was published in volume 5 of the journal *Respiration Physiology*.

Wallace Fenn will not be forgotten. During his unusually long and productive career he influenced in his quiet and selfless way many friends, colleagues, and students, both at home and abroad. He will always be admired and remembered as a great pioneer in physiology. He was always one step ahead of most,

* "Respiration Suite," *The Physiologist*, 6(1963):47–48.

and when he plowed a virgin field his furrow was straight and deep so that followers would not lose their way.

I AM GREATLY INDEBTED to Mrs. W. O. Fenn, Miss Augusta Dustan, Drs. Arthur Otis, Albert Craig, Pierre Dejours, Harry D. Bouman, Paul Horowicz, and Loren J. Mullins, and many others for sharing their remembrances.

AWARDS, HONORS, AND DISTINCTIONS

CHRONOLOGY

1893	Born August 27, Lanesboro, Massachusetts
1910	Graduated from Cambridge Latin School, Cambridge, Mass.
1914	A.B., Harvard University
1916	A.M., Harvard University
1917–1918	Second Lieutenant, U.S. Army, Sanitary Corps
1919	Ph.D., Harvard University (Plant Physiology)
1919–1922	Instructor in Applied Physiology, Harvard Medical School
1922–1924	Traveling Fellow, Rockefeller Institute, A. V. Hill's Laboratory and H. H. Dale's Laboratory, London
1924–1959	Professor and Chairman of Physiology, The University of Rochester School of Medicine and Dentistry
1962–1966	Director, Space Science Center, The University of Rochester
1961–1971	Distinguished Professor of Physiology
1971	Died September 20, Rochester, New York

MEMBERSHIPS (selected)

National Academy of Sciences (elected 1943)
American Philosophical Society (elected 1946)
American Academy of Arts and Sciences (elected 1948)
The American Physiological Society (President, 1946–1948)
American Institute of Biological Sciences (President, 1957–1958)
Society for Experimental Biology and Medicine (President, 1957–1959)
International Union of Physiological Sciences (President, 1968–1971)
International Academy of Astronautics
Undersea Medical Society
New York Academy of Sciences (Fellow)
Rochester Academy of Science (Fellow)

HONORARY MEMBERSHIPS

1928 Harvey Society
1929 Alpha Omega Alpha
1951 Sociedad Argentina de Biologia

1961 Honorary Life Fellow, Rochester Academy of Medicine
1963 Italian Society of Experimental Biology
1965 Canadian Physiological Society
1965 Physiological Society of Great Britain
1965 Foreign Member, Accademia Nazionale dei Lincei (Rome)
1970 Academie Royale de Medecine de Belgique
1971 Rochester Museum and Science Center

AWARDS

1949 John F. Lewis Prize, American Philosophical Society
1958 Gold Medal Award, University of Rochester Medical Alumni Association
1961 Certificate of Merit, Rochester Academy of Medicine
1964 Daniel and Florence Guggenheim Award, International Academy of Astronautics
1964 Antonio Feltrinelli International Prize for Experimental Medicine, Accademia Nazionale dei Lincei, Rome
1966 Modern Medicine Award for Distinguished Achievement, Board of Editors, *Modern Medicine*
1967 Research Achievement Award, American Heart Association
1971 Johannes Müller Medallion, The German Physiological Society
1971 Ville de Monaco Medal

HONORARY DEGREES

1950 University of Chicago, D.Sc.
1959 Universidad San Marcos, Peru, Catedratico, Honorario
1960 Université de Paris, Docteur Honoris Causa
1965 Université Libre de Bruxelles, Docteur (Hon.)
1965 The University of Rochester, D.Sc. (Hon.)

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1919

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1921

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1922

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1923

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1924

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1925

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1926

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1927

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1928

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