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EDMUND NEWTON HARVEY

1887—1959

A Biographical Memoir by
FRANK H. JOHNSON

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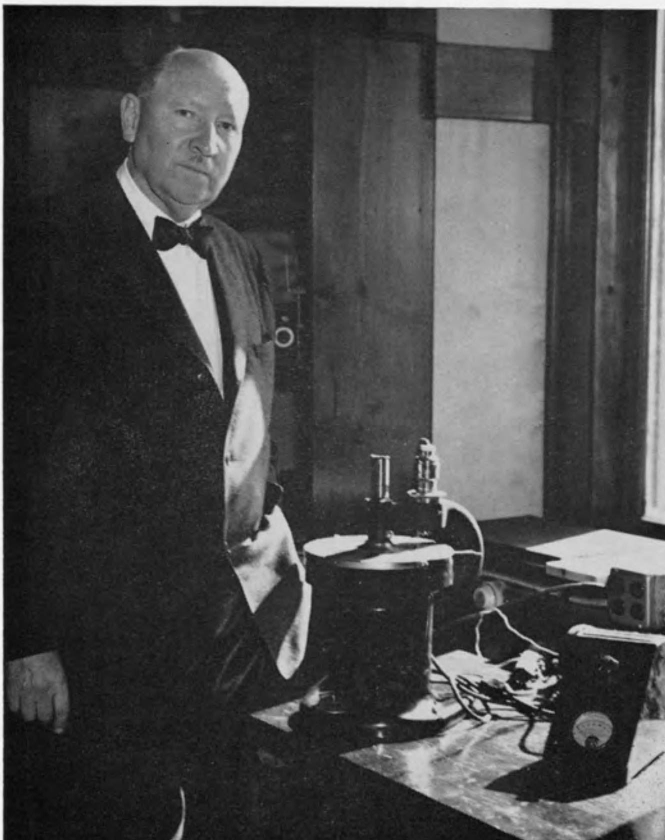

E. Newton Harvey

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November 25, 1887–July 21, 1959

BY FRANK H. JOHNSON

IT HAS BEEN aptly remarked that no man makes an institution, but if that is true, Edmund Newton Harvey during his lifetime came very close to establishing an exception to the rule. He was the acknowledged Dean of Bioluminescence; no one ever has matched, and perhaps no one ever will, his widely encompassing, scholarly contributions to our knowledge of the mystifying natural phenomenon of the emission of visible light by living organisms, which stimulated his greatest interest and research activity, his boundless energy, and his contagious enthusiasm. Yet in reality this was only one of his specialties, for at the same time his imagination and ingenuity found productive outlets along other avenues of cellular and comparative physiology, biochemistry, biophysics, and broader aspects of biology, mostly from a purely basic point of view, though also, when circumstances demanded, with a view toward the more immediate practical significance in such areas, for example, as wound ballistics and aviation physiology. His own distinguished research in many fields of endeavor, the students and professional associates whom he inspired, the laboratories over which he held sway, the four corners of the world in which he conducted original investigations and gave invited lectures, and the virtual synonymy of his name with the general subject of bioluminescence add up very nearly to the attainment of a one-man institution.

Precisely when his rather fabulous career may be said to have begun is a matter of definition, opinion, and interpretation. His autobiographical notes are fascinating to read and they reveal some of the factors which early channeled his intellectual pursuits into the field of biology and molded the character, disposition, and personality of the mature scientist who became so well known, respected, and admired. Clearly, he was born with an alert, impressionable mind, with a capacity for analytical thought and logical decisions. His place of birth was suburban Philadelphia, at a time of staid social conventions and religious emphasis. His father was an Elder of the Presbyterian Church and prominent in Sunday School affairs, but he died (1893) when Harvey was six years old, after which the embryo scientist grew through childhood in the care of his devoted, tolerant, and understanding mother and three older sisters. The following excerpts from notes on "Earliest Recollections"[1] written late in life show, on the one hand, that his first, most lasting impressions were of a biological and scientific nature, and, on the other hand, that his somewhat precocious drift away from religious dogma, accompanied nevertheless by development of a keen sense of ethics, a solid integrity, impeccable taste, and a dignified sense of humor, began at a tender age indeed.

"Probably my earliest memory is of tadpoles in an aquarium (containing green water plants and a stone castle-like object) in my nursery. Later I wrote an essay on tadpoles referring particularly to their spots, but this effort has been lost. I also remember an electric motor which would revolve when the base (of two different metals) was placed in salt solution.

"We lived in a large stone house on W. Upsal Street, Germantown, Pennsylvania . . . surrounded by several acres of land. . . . There were many plumbing fittings and iron pipes left

1. The author is indebted to Mr. Eugene Kinkead of *The New Yorker* for a copy of these unpublished notes.

over from the house, and I spent my time on a vacant lot next door installing these pipes in foundations I had dug for a new house. No doubt this behavior indicates an early interest in 'do it yourself,' in mechanical things and in use of the hands. I always had a set of carpenter's tools which were much used." As Dubos[2] has pointed out with respect to Pasteur, Harvey ultimately "put into practice Benjamin Franklin's admonition that a good workman should know how to saw with a file and to file with a saw."

"I had to attend both church and Sunday School. I can still recall clearly the walk to and from church, the long sermon, and my restlessness, when I wanted to be outside collecting things. [This was evidently before he was six years old.] Sunday School bored me and I only remember a certain interest when the teacher explained that Nicodemus had to be born again in order to be saved. My literal interpretation of this story, which seemed to transcend observed facts, started my skepticism of other teachings, and I fear the religious view of natural phenomena soon aroused a certain antagonism in me. . . . I continually heard talk of church affairs and how money could be raised for this or that good cause. Foreign missions were also a special interest of our church. Such talk was rather distasteful to me, as I could not see how conversion to Christianity would help the Chinese or Japanese, who already had a highly developed system of ethics, which suited very nicely the elaborate culture and dense population of these nations. Nevertheless, this talk instilled in me a distaste for raising money, which has persisted and been the main factor in my refusal to accept those executive positions in which money raising is one of the duties of the office."

Despite an early agnosticism and some rebellion in regard to formal religion, he records appreciatively that "my mother

2. R. Dubos, *Pasteur and Modern Science* (Garden City, N.Y., Doubleday and Co., 1960), p. 52.

taught me strict honesty in all things and a particular dislike of insincerity and hypocrisy, which probably explains my lack of interest in political affairs. . . . I have no ability to say nice things to a person I do not admire. [In all fairness, it should be recorded that, conversely, he made it a point not to say anything unkind to, or derogatory about, anybody.] My mother also stressed the golden rule, which I still believe to be one of the truly great ethical precepts, which everyone should consider before action of any kind."

After his father died, his family moved to another home, where Harvey lived until his departure to Columbia University for graduate study. His room on the third floor became filled with "various collections of bird's eggs, minerals, insects, etc.. . . There were a few live animals in my collection—frogs in the family bath-tub to lay eggs in the spring—but mostly my acquisitive instinct ran to things which could be preserved indefinitely, i.e., material for a museum rather than a zoo. . . . Later I collected every conceivable natural object."

His collecting activities continued throughout his life, eventually comprising an inventory beyond the capacity of most mortals to catalog in less than a full-time job. In adult life, natural history specimens dwindled to a quantitatively minor role among his acquisitions, as his interest focused on the experimental approach in biology. From the time he came to Princeton as an instructor in 1911 until he became Professor Emeritus in 1956, he accumulated a vast array of apparatus, electronic equipment, specially designed glassware, gauges, electric motors, photographic equipment and supplies, precision optical devices, tools, relays, galvanometers, unusual chemicals, and miscellanea such as metal tubes, rods, sheets of cork, plastics, etc., which filled numberless drawers and cabinets in his office and adjacent laboratory rooms. Included also among the various items were a considerable number of plumbing fixtures such as iron pipes, threaded elbow-joints, and T-connections. All were stored away because of past application or potential usefulness. Remarkably enough, even though some of the multitude of items may never have been put to use, many of them did indeed "come in handy." More remarkably still, he always knew what was there and where to find it. The same was true in regard to his voluminous papers, memorabilia, and *objets d'art*. He had a fantastic memory for particular details which interested him in one way or another, combined with a rare ability to discriminate effectively in omitting superfluous details from his discussions, lectures, and writings.

The first formal lecture in his professional career was delivered in April of 1911, on invitation from the Department of Biology at Princeton. The subject was "The Permeability of Cells," based largely on his dissertation for the Ph.D. degree which he attained in June of the same year, after only two years of graduate work at Columbia University under Thomas Hunt Morgan. His graduate work followed directly upon four years at the University of Pennsylvania, where he distinguished himself for his versatile activities in biology and other sciences and where in his junior year his life's interest in General Physiology was kindled in a course on this subject given by Professor Ralph Lillie. At Pennsylvania he studied also under Professors H. S. Jennings and E. G. Conklin, the latter of whom left in 1908 to become Chairman of the Department of Biology in Princeton. Harvey's competence, talents, and promising future were familiar to some of his audience in his first lecture and were easily recognized by others. He was promptly offered, at the age of twenty-three, the position of Instructor in Biology, effective the forthcoming academic year, and he remained, from then on, officially and faithfully associated with Princeton, though there were numerous occasions when his home institution seemed more in the nature of a home base while he was away on extended expeditions.

Although no one now can give an account, from personal experience at the time, of the impression he made as a young instructor, those of us who have had the privilege of knowing him well in later years can easily picture him as a tall, thin but athletic, quiet, dignified, slow-speaking but fast-thinking, well-poised, polished-mannered, handsome young man, young enough in fact (as he once recalled to the writer) occasionally to be mistaken for a freshman on the campus. Some ten years after his first year at Princeton, a photographic portrait published in *World's Work* reveals a still notably youthful appearance with a pensive, almost poetic expression. None of these personal attributes reflected the rugged life he had spent on expeditions, his love of travel and the great outdoors, his vigor in certain sports such as tennis and handball, his wealth of knowledge and laboratory experience, or the energetic drive and breadth of penetrating biological studies that he brought to his first faculty appointment in 1911.

The unabated continuation and efficient expansion of these activities and interests resulted in a momentum-gathering, meteoric rise through the academic ranks, within the space of eight years, first to Assistant Professor in 1915, then, completely hurdling the normally intermediate stage of Associate Professor, to full Professor in 1919. During this period, despite the relaxed deliberation that characterized his demeanor and temperament, he successfully assumed rigorous teaching responsibilities on both graduate and undergraduate levels, including not only areas appropriate to his chosen field but also others such as hygiene and bacteriology arising from the needs of World War I. At the same time he produced an imposing list of technical publications, a laboratory manual of general physiology (1913), and his first book, *The Nature of Animal Light*

(1920). An especially noteworthy addition to his teaching responsibilities was made in 1920 when he introduced into the curriculum of the department a course in biochemistry, for this was surely one of the first nonmedical, undergraduate courses on the subject to be offered at a liberal arts college in this country, and it is a tribute to his foresight that he so soon recognized the importance of such a course to a fundamental knowledge of biology. He continued to give the lectures and supervise the laboratory instruction in this course for the next twenty years, when it was given over to his associate, A. M. Chase. While the content has been modified in keeping with advances in theory and methodology of the science, the course still fulfills a significant role in the now greatly expanded program of education and research in the biochemical sciences at Princeton.

In his early professional life, two events of overshadowing importance to his future took place. The first, in 1913, was the definitive arousal of his interest in bioluminescence, and the second, in 1916, was his marriage to Ethel Nicholson Browne. The former of these events, which is referred to again in later paragraphs, occurred during a three month's stay at Murray Island near the nothernmost end of the Great Barrier Reef of Australia. The latter event marked the beginning of a successful combination, on the part of both husband and wife, of professional pursuits and raising a family. Ethel Nicholson Browne had completed her doctorate in biology at Columbia University in 1913 and had held instructional or research appointments at Princeton, California, Cornell, and elsewhere; the distinguished career which she was to achieve in her own right was already well launched. Within six years of their marriage they had two sons, Edmund Newton Harvey, Jr., and Richard Bennet Harvey, destined also for successful careers in science and medicine respectively.

Amidst the numerous responsibilities and activities of these years, Harvey traveled widely. In 1912 he went to Italy, Austria, Switzerland, Germany, Norway, and England; in 1913, on an expedition with Alfred G. Mayor, to the Great Barrier Reef of Australia, to Tahiti, Raratonga, Wellington, Sydney, Brisbane, Townsville, Cairns, Thursday and Murray Islands in Torres Strait (it was here that his special interest in bioluminescence developed), American Samoa, and Honolulu; in 1915 to Cuba; in 1916, with his bride, to Japan, where they visited Uotsu on the west coast to collect and study the luminous squid *Watasenia* and then walked by way of the high mountains to Tokyo, proceeding on to the Marine Laboratory of the Imperial University at Misaki, where he first became acquainted with the tiny, luminescent crustacean *Cypridina*; in 1917, again to Japan for further study of *Cypridina* and travel through Korea, Manchuria, Peking, Shanghi, Hong Kong, Macao, Canton, and Manila; and in 1919 to the Dutch East Indies, stopping in route for study of luminescent organisms at the Friday Harbor Marine Laboratory, Washington state, thence to Vancouver, and by ship to Yokohama and further travel to Kobe, Nagasaki, Shanghai, Hong Kong, Singapore, Batavia, Semarang, Surabaya, Bali, Lombok, Sumbawa, Macassar, Amboina, and finally the Banda Islands. In the Banda Sea he found the small, luminous fishes *Photoblepharon* and *Anomalops,* whose light he concluded, on indirect evidence, arose from symbiotic luminous bacteria in their photogenic organs, an interpretation that remains to be firmly substantiated through experimental approaches that were not available at the time. From the Banda Islands, his return trip was by way of Singapore, Penang, Colombo, Aden, Suez, Port Said, and Marseilles to Monaco where in December 1920 he joined his wife and their four-year-old first-born son, Edmund Newton Harvey, Jr., for a brief stay at the Oceanographic Institution before sailing for the United States to resume his teaching duties.

World travel and prodigious work during this period were not new to Harvey, and whether in travel or in the laboratory no sharp distinction can be drawn between what to him was recreation and what was work. Amidst his ceaseless activity he knew how to relax as well as to work and he enjoyed to the fullest the two indissociable phases of his life. While his real claim to fame rests upon his scientific achievements, which are referred to more specifically in later paragraphs, he should be long remembered also, like Samuel Johnson, as a man of extraordinary personality and influence among his peers and followers. A further glance at his younger days will serve to make the picture clearer, for much of what he became was presaged in his early youth, and here again his own words are most interesting. His "Earliest Recollections" contain nostalgic, but also illuminating, reminiscences of his preparatory school, such as the following.

"In looking over the group pictures in 'Ye Primer of Ye Germantown Academy of Ye Class of '05,' I discover a group of healthy, attractive (many of them handsome) American Boys, whose innocent looks belie the devilishness that went on from time to time both in and out of class. In going upstairs from one recitation to another, it was always necessary to protect the rear end from paddles by those behind. For years afterwards I found myself placing a protecting hand across the seat of my pants whenever I preceded a companion up a stairway. [This gesture against playful assault recurred occasionally all his life, in utterly invulnerable circumstances, as when standing by his desk or laboratory table, lost in reflective thought, or even during a lull in conversation at social gatherings.] The most amazing result of my perusal of 'Ye Primer' was the discovery that I could still remember perfectly the names of almost all members of the class, although I have never revisited the school. . . . I toyed with the idea of returning to school for the fiftieth reunion, in 1955, but decided against going on the ground that too many years had passed. . . . My attitude toward reunions. . . is merely a reflection of my concern with things rather than people, especially people *en masse.* I dislike crowds, and when a scientific society becomes too large, I lose interest in it. . . . Among other things which I discovered in 'Ye Primer' was the fact that I was Athletic Editor of the Academy Monthly, played on the tennis team, was a soldier in the Belfry Club (a minor part if there ever was one), Chairman of the Ivy Committee (whatever they did), and a member of the Philo, the debating Society. The latter was surely a dubious honor, as everyone belonged to Philo, and I hated debating and also reciting." (It is interesting to note that throughout life he made it a point never to become embroiled in a controversy.)

"There was no music taught at Germantown Academy; the purpose of this school was to prepare young men for college." In spite of home influences at the time, and later association with well-known artists during summer vacations in the Catskills, he remarks that "my own education in both music and art was absolutely nil. Only as a graduate student at Columbia University in 1909-1911 did I attend grand opera, sitting in the peanut gallery of the Metropolitan. . . . Opera has never appealed to me as has symphonic music, the louder the better (within limits). Interest in art was a much later development, and I must confess that even today my chief concern with art is to try and discover why certain pictures are highly regarded and others not—a purely scientific approach. The Museum of Modern Art is so conveniently located in mid-town New York that I drop in there on every occasion, almost like a club, to see what is new in the grotesque (to me), and try to figure out why a particular work has received a $5,000 prize.

"While I was still a student at Germantown Academy, there occurred one episode whose meaning or origin I cannot understand—a sudden desire to learn—not merely about natural history, which already had my complete interest, but about all sorts of things, perhaps most strongly the origin of words. I collected etymologies and dictionaries for my room, and consulted our encyclopedia so frequently and so persistently that my family got worried. . . . Finally I decided that the acquisition of all knowledge was too much, and decided to stick to science, which became almost a religion with me. . . . Since there was no science taught at Germantown Academy until the last year, when a brief course in chemistry was inaugurated, my early scientific learning was all self-taught. . . . It was only on entrance as a freshman at the University of Pennsylvania in 1905 that I was able to satisfy my longing for additional knowledge in all fields of science, in biology, in geology, mineralogy and paleontology, in physics and chemistry and in psychology."

During boyhood, summers were never spent in Germantown, but in various other places including Nova Scotia, Vermont, Martha's Vineyard, and Long Island, followed by successive seasons at Arkville, in the Catskill Mountains of New York, where his relatives ran the Pakatakan Inn and he "spent the really superb time" of his youth. His sensitivity to the grandeur of scenery and the beauty of unspoiled nature, and his healthful activities of mountain climbing, blazing trails, and camping, interspersed with collecting botanical as well as zoological specimens, are vividly recounted in his "Earliest Recollections." He remarks that "it was great training for later summers in the Canadian Rockies . . . in order to penetrate really wild and unmapped country. . . . There was a tennis court on the place and tournaments were held, so that I had plenty of practice. There was also a 'swimming hole' in the river where I learned to swim, but tramping and hiking supplied most of the exercise. . . . The food was superb."

Throughout his life he retained a profound appreciation of good food, and as an adult he never turned down an invitation to a good dinner in desirable company if he could manage to attend; he kept a pocket notebook containing the addresses of choice restaurants and other places to eat in the cities. He enjoyed having a cocktail or two before dinner but never drank too much, just enough to unleash his normally somewhat constrained but keen sense of humor which then surged forth in spontaneous, effervescent mirth and mildly explosive bursts of captivating laughter. Referring to the annual summer masquerade party during his youth at the Pakatakan Inn, he remarks that "no liquor was sold, and I doubt if any guests had a private supply, so that I now look back with some amusement to observe how jolly a gathering could be without cocktails."

University life began when he entered the University of Pennsylvania as a freshman in 1905. He became at once so enmeshed in scientific pursuits that he participated in virtually no social activities beyond associations in class or laboratory. In his words, "As I was only interested in Science, I felt no need for anything else. I did not endeavor to join a fraternity, but did take an interest in football, attending all the games at Franklin field, probably a hangover from my Germantown Academy days as athletic editor of the Academy Monthly. I also played some tennis."

His "extra time" was spent either in collecting specimens relevant to his interest in systematic biology or in studying specimens at the Academy of Natural Sciences in Philadelphia, where he became imbued with an abortive ambition to become a specialist in the Myriapoda, i.e., to become an international authority on centipedes. He did not go a long way in this direction, but he was eventually rewarded by having a centipede named after him (*Pselloides harveyi,* Chamberlin, 1942), as well as a luminous bacterium (*Achromobacter harveyi,* Johnson and Shunk, 1936) and a firefly (*Photinus harveyi,* Buck, 1947). Although his predilection for systematics gave way, within a couple of years, to the fulfillment he found in experimental biology, the viewpoint of classification was indelibly stamped on his scientific outlook and it influenced the approach he adopted in both writing and research. It provided, for example, the organizational framework of his book *Bioluminescence* (1952), for which he undertook to collect and review every publication on this subject between the years of about 1850 and 1950, and which resulted in an invaluable reference work. In experiments he tended to carry out an orderly investigation of factors and subfactors bearing on the problem at issue. The discovery of new facts was justification in itself of the effort involved, and while the data pertaining to complex systems often required a rather phenomenological treatment, they were placed in the context of existing information as logically and securely as knowledge available at the time permitted.

The transition of his interest from an emphasis on structure and systematics to one on function and general physiology was somewhat gradual and altogether natural. It was becoming evident when he studied as a freshman under the botanist Professor John MacFarlane, whose special interest was sensitive and insectivorous plants and who kept a greenhouse full of them—*Mimosa,* sundews (*Drosera*), Venus's-flytraps (*Dionaea*) American pitcher plants (*Sarracenia*), and the large Malayan *Nepenthes,* which was alleged to catch animals as large as mice and bats. Harvey was particularly intrigued to observe, in the sensitive plant *Mimosa pudica,* how "the pairs of leaflets on a compound leaf fold up one after another, when the outermost pair were touched, and to follow the impulse for closing of leaflets as it moved down each row of leaflets, through the leaf stem to the pulvinus of the main petiole. This pulvinus was at the junction with the stem of the plant; it contained a mechanism for endlessly changing the leaf from an upright to a drooping position. The whole leaf suddenly wilted. Such motor activity in a plant is quite analogous to nerve muscle activity in animals, and probably started my lifelong interest in the nerve impulse and nerve phenomena of various kinds. In later years, all graduate students at Princeton University knew that they would surely be asked to explain the nature of the nerve impulse on their Ph.D. oral exam."

In his freshman year, Harvey was given part of a table (a privilege he retained throughout his four years at Penn) in a room on the top floor of the biology building which was shared by Professor MacFarlane's assistant and others. He learned to cut sections by hand with a razor to study plant histology, as well as to record quantitative data in experiments with sensitive plants, such as the rate of the impulse for closing leaflets, the slow revolving of the apex of the plant during growth from day to day, etc. Understandably, he was chosen by MacFarlane as one of two student assistants on a trip to Europe the following summer.

Their trip to Europe in the summer of 1906 had only the most modest financial support, and demonstrated Harvey's adaptability to situations imposed by the circumstances involved in the work to be performed. They spent a brief period in London, visiting Kew Gardens every day, where MacFarlane worked in the herbarium, then left for the Austrian Tyrol and Switzerland to collect alpine plants. They experienced "no luxury travel, no wagons-lits, no waiters with white gloves hovering about a splendid table. . . . We sat up in trains overnight, stayed at modest Gasthaüser, where a spotlessly clean room could be had for 0.25 a night, or even slept at peasant farmhouses, right next to the cows. . . . Collecting plants was hard work. There was not only the vigorous exercise of attaining some inaccessible spot for a rare species of fern, but with the day's collecting done, the plants had to be selected and pressed, the blotters dried in the sun or by a fire, and the final specimens bound for transportation. . . . In later years, I have had trouble convincing my friends that I was ever a botanist or even interested in botany . . . but I have always regarded plant cells as equally favorable or more favorable than animal cells for physiological research. My Ph.D. thesis on 'The Permeability of Cells' at Columbia University in 1911, although granted in a Zoology Department, contains as much on plant as on animal cells. For the physiologist, which I finally became, plant and animal cells function in essentially the same way and are both useful for the solution of physiological problems."

His interest in zoology broadened in his freshman year, especially in the general course given by H. S. Jennings. He found his first view of *Paramecium* exciting, at "seeing these slipper animalcules darting in the field of the microscope and behaving in every way as if they were intelligent beings with work to do and a purpose in life. . . . much of my spare time after this occasion was spent in collecting scum and debris from all the streams and ponds of the neighborhood and making a large collection of permanent microscopic slides of the organisms found, a collection for which I later received a prize."

Further study of the morphology, histology, and embryology of higher animals as well as plants had to await his sophomore year, again under John MacFarlane, H. S. Jennings, and also others, notably E. G. Conklin. He dissected the cat "from tip to toe" and read St. George Mivart's book on this animal "from cover to cover." A year later, his interest in general physiology permanently crystallized in a course given by Ralph Lillie, whom he credits as the one man who determined his final career as a cell physiologist. "Physiology was a direct approach to the workings of the cell itself, unit of all living things; an attempt to explain functional activity of organisms in terms of chemistry and physics, what seemed to me a rational approach to every problem of biology. Jacques Loeb's 'The Dynamics of

Living Matter' had just appeared, in 1906, and I now feel that Lillie and I were both greatly influenced by Loeb's materialistic view of biological problems. There was no doubt that I had found my proper approach to the great subject of biology, having advanced in my own personal career by the same path that historical knowledge of living things has taken. First came collectors, then systematists naming the species, then morphologists studying gross structure, then histologists concerned with the fine structure of tissue and the cell, then the chemical and physical properties of the material making up the cell. For want of a better word, this material usually goes by the old-fashioned name of protoplasm. Loeb's definition of living organisms as 'chemical machines, automatically capable of maintaining and reproducing themselves' appealed greatly to me, and is still as good a definition as can be found. The modern physiologist is inclined to speak of cell investigation 'at the molecular level,' but all he means by this is that a study of the biochemistry and biophysics of materials in the cell will be undertaken. In later years I came to know Jacques Loeb and Ralph Lillie very well from contacts at the Marine Biological Laboratory at Woods Hole, Massachusetts, and grew to like and admire them more and more."

The summers following his sophomore and junior years, in 1907 and 1908, offered further opportunities for field experience, on both occasions in the Pacific Northwest, chiefly in the high alps of British Columbia, where at times his life was rugged indeed, a combination of real adventure and some incidents of tragic or near-tragic consequence. Both times he was an assistant to the botanist Dr. Charles Shaw, and there were other members of the expeditions, including Merkel Henry Jacobs, whom he had known at Penn.

"The two summers involved an unusual toll of tragedies. A friend of Jacobs, Edward Heacock, was drowned in an attempt to recover a cache of food left during a previous trip. Jacobs broke his leg above the tree-line, and had to be dragged down to timber by Heacock and made as comfortable as possible in a pup-tent, then left alone for three days while Heacock made his way to civilization to obtain help. Shaw was drowned a few years later when his canoe upset on the Columbia river. It is a wonder more of us weren't injured by falling stones as we passed gullies and chimneys on rock climbs. . . .The breaking of Jacobs' leg could have been another tragedy. Jacobs and Heacock had gone out to British Columbia early in June, 1907, in an attempt to climb what we all called 'The White Elephant,' a snow-clad peak in the center of the Big Bend region (now Mt. Sir Sanford) which was not even marked on maps. We talked a lot about this mountain and how to get to it and conquer it—whether by canoe, north of the Columbia river from Beavermouth, or whether overland through the east ridges of the Big Bend region. For the latter routes, the trip was about six miles by railroad from Beavermouth, then a trek north through the mountains. Engineers of the C.P.R. were obliging in those days, and would give us lifts on their pusher engines (needed to push trains up the steep slope to the divide at Illecillewaet Glacier), and would stop to let us off wherever we wished. That is the route Jacobs and Heacock took, and the route by which Heacock returned for help, having flagged a train when he finally reached the railroad.

"Heacock found us at Field in the afternoon and we (Shaw, a Canadian medical student, who was the only person with any medical experience we could find, Heacock, and I) started off. We took a night freight to Beavermouth, and I remember particularly looking at the stars from an open freight car and feeling a real thrill of adventure in rescuing an injured man. At Beavermouth we got a little sleep in some empty cabins and set off early in the morning on a pusher engine, which let us off at the usual place for the long trek to where Jacobs lay. For food he had only cold oatmeal cooked the day Heacock left.

"We all carried heavy packs, which in addition to their actual weight are likely to throw one off balance in stepping over any obstacles. There were plenty of obstacles and no trail whatever—innumerable large tree-trunks, the trees killed by fire and then toppled by wind, alder thickets thru which one had literally to force a way. If these alders grew on a fairly steep slope, they were almost impassable, as one had to force and climb at the same time. Then there were the mosquitoes, real pests in the daytime. They even follow one above snow-line, and I have frequently drunk soup through a mosquito net to protect myself. Add to all this the necessity for haste, and one can visualize the hardships of this particular march. Finally we did attain altitude and reached what we called the 'boardwalk,' above tree-line, a series of up and down ridges with relatively gentle slopes, only an occasional snow field to cross. This was easy going, and after a few more hard climbs we finally reached Jacob's tent about dusk, and found him all right. However, the sky had clouded over and soon it began to snow, not heavily, but enough to make things disagreeable without cover. We did not even have a tent. We decided not to try to set the leg until morning. It was a terrible night. . . . At last the morning came and I think it stopped snowing. We gave Jacobs plenty of whiskey and the medical student set his leg as best he could and we made him as comfortable as possible with hot food and the cheer of companionship. I slept most of the time, whenever I was not needed, and the next day Shaw and I left for the railroad again to get more help. I cannot remember the details of what happened after that but Jacobs lay in his pup-tent all summer. Books were brought in, and he became proficient in calculus and other scientific matters. He was carried out on a stretcher in late August by his brother Bob, Shaw, [Herbert]

Ives, Fred Martin, and his father (of Beavermouth), again in a snowstorm, at the railroad he was placed on the cow-catcher of a pusher engine and finally arrived in civilization at Beavermouth, a town of a few houses and many empty shops."

On the less arduous side, Harvey recalled that "the Canadian Rockies and Selkirk range were perfect for camping. . . . There were bears, caribou, mountain goats, marmots, porcupines, and ptarmigan. I always carried a 30-30 rifle as much for support in climbing as for shooting, although fresh meat was a great luxury when most of our food was dried material (flour, oatmeal, rice, erbswurst, prunes) and bacon. . . .

"Perhaps the most enjoyable time in British Columbia was the year . . . Dr. Shaw decided to go up the west arm of the Columbia river and then move east into high mountain country along one of the little streams that feed the Columbia. . . . For this trip, pack horses were necessary (cayuse as they were designated in B.C.). We hired several of these and a man to care for them, collected our duffel, and embarked on a funny little sternwheeler, which made an occasional trip from Revelstoke to Downie Creek and return. The trip up the Columbia was into primeval forest, which must have been exactly like the scenery which confronted early western explorers, such as Lewis and Clark, except that there were no Indians. The trees were great Douglas firs and the underbrush very dense—alders and Hercules Club or Angelica tree, a species of Aralia, with strong pointed spines. We nosed upstream and finally ran the bow of the boat into the bank at a likely spot evidently known to the steamboat captain. Here we all debarked, luggage, horses and their owner, and a group of some eight people in the Shaw party. When the boat left, the first thing we discovered was that our cayuse-man must have imbibed rather freely on the voyage, for he could hardly walk and soon went sound asleep. We gave him the heat treatment, covered him with blankets until he practically sweated out the alcohol, and finally came to.

"I don't recall the details of our journey into the wonderful alpine meadows back of the river, but we finally came out on lovely grass meadows with many patches of snow still left. . . . there is no doubt that these were halcyon days, even when it rained, which it frequently did. One of my most vivid memories of British Columbia is trying to dry out in front of a hot fire in the open, with my wet clothes still on me and all the scenery enveloped in fog. To be contrasted with this was the campfire at night, with our little group sitting around it, and the clusters of tall spruce trees silhouetted against the sky and the stars.

"When the sun came out, the meadows all about us were transformed with flowers, pushing up even through the edge of a snow drift; the air was warm and the sun could burn. . . . Ice-cold mountain streams gave pure drinkable water anywhere and ice-cold ponds allowed us to bathe—that is, a sudden dip and even more rapid exit. We had plenty of fresh caribou and lived in style. These are the rewards for hours of sweat and fatigue and back strain under a heavy pack, while trying to reach a destination which may not be of particular interest after arrival. During rest periods, we often discussed the philosophical question as to why we did this, why we ever came to such a cursed country in the first place, and vowed that this would be the last time that British Columbia or any mountain region would ever see us. There is, however, something that takes one back, and I note that in the long run the hardships are forgotten and only pleasant memories remain."

As fate would have it, the very next summer found Harvey at one of the flattest areas in the world, though surely not because of any deterioration in his profound love of lofty mountains, which he visited time and again in different parts of the globe, albeit in increasingly comfortable circumstances befitting an advance in years. It just happened that in 1909

Dr. Alfred Goldsborough Mayor, Director of the Dry Tortugas Marine Biological Laboratory of the Carnegie Institution of Washington, needed a summer collector. Harvey was recommended for the job and duly appointed to it. This was a fortunate event, not only because it provided Mayor with an unusually capable assistant, but also because it introduced Harvey to an intimate acquaintance with marine biology and established a firm, companionable friendship between the mature scientist who headed the laboratory and the brilliant young general physiologist who was just approaching the threshold of his professional career. Mayor had been trained as a systematist at Harvard, had traveled widely with Alexander Agassiz, was thoroughly acquainted with the South Seas and other parts of the world, and, when Harvey first knew him, was finishing his three-volume, monumental work on *Medusae of the World,* illustrated by his own exquisite drawings. At Tortugas, Mayor's interests had turned particularly to physiological studies of the large jellyfish, *Cassiopea,* which Harvey also used later as an especially favorable organism for investigating certain aspects of nerve function.

The trip to Tortugas began in New York, on a small, coastwise steamer to Key West, Florida, and it is more than a casual detail, with respect to Harvey's future interests, that the darkened decks of such ships at night afforded a clear view of the so-called phosphorescence of the sea. Also, with his characteristic avidity for learning all things scientific, Harvey was stimulated to study the different facets of the nautical world. At Tortugas he learned to use a sextant and calculate the latitude of the island with a remarkable accuracy; he read Bowditch assiduously; he learned about ocean currents and winds, the horse latitudes and the region of trades and doldrums, and the sail rigs of various types of ships.

Tortugas was reached, some eighty miles beyond Key West, by means of the twenty-ton laboratory yacht *Physalia.* The destination could scarcely have provided a greater contrast to the mountainous regions and way of life of the previous summer in British Columbia. At the time, there was no electricity and no means of refrigeration on Loggerhead Key where the laboratory was situated, and apart from fresh fish, practically the only food considered safe to eat was canned; a pill was dispensed "whose effect was such that I am sure no amoebae of dysentery could cope with it"; the warm, iron-tasting drinking water was collected from rain on the laboratory roof; the weather was consistently hot and humid, including days of flat calm when not a breath of wind could be felt and the distant horizon could be discerned across a glassy sea. There were also many pleasanter, sunny days, interspersed with local storms, squalls, and drenching thundershowers. On at least two occasions Harvey's life was perilously endangered while he was collecting, but fortunately no serious mishap occurred. On the whole, he adapted himself so fully to the circumstances in general that he felt that "life suited me exactly." Moreover, he carried on rewarding activities in both collecting and research; his first scientific publication (1909), entitled "Membrane formation and pigment migration in sea urchin eggs as bearing on the problem of artificial parthenogenesis," was in fact based on work at Tortugas and later experiments performed the same summer at Woods Hole, Massachusetts. At Garden Key, a few miles from Loggerhead Key, he "was introduced in a most intimate manner (i.e., no casual glance from a glass-bottomed boat) to the wonderful fauna of the tropics. The water was crystal clear, the animal life new and bizarre. I was a collector in paradise. In a very short time I came to know the best collecting places for the forms that were needed, and by midmorning [after getting up at dawn] could return to the lab, deliver my goods, and then start research of my own."

Mayor prudently closed the laboratory about the first of August, at a time of unbearably hot, calm weather and the beginning of the season for devastating hurricanes. A slow boat was again taken on the return trip to New York, and Harvey proceeded further northwards for his first visit to the Marine Biological Laboratory at Woods Hole on Cape Cod, to continue his research on invertebrate eggs. This laboratory, which now holds the topmost position of marine laboratories in the world in terms of scientific facilities, distinguished members and visitors, educational program, and other features, was not much beyond the start of its destiny in the summer of 1909. At that time, it had no brick buildings, no electricity, there was "no street lighting at night, practically no stores and no place to eat except the laboratory mess. We either roomed in town. . . or rented a cot on the top floor of the 'stone building' with about 12 other young men, many of whom were crewmen and had to arise around 5:30 A.M. to get to work. They saw to it that everyone else in this 'dormitory' knew that they were awake." One cold-water faucet at the head of an outside stairway "was used for washing the face and hands, as well as to sprinkle anyone who was a little slow in rising. All bathing was done in the sea."

In addition to the work which he zealously pursued without the lavish equipment and modern accommodations that many present investigators consider essential, at Woods Hole Harvey met most of the great biologists of the time from the eastern United States. In later years he built a cottage near the laboratory and ultimately acquired a delightful summer home on Penzance. From 1909 through the rest of his life he spent a part of every summer in Woods Hole.

With the awarding of his B.S. degree in June 1909, Harvey's undergraduate days ended. He had enjoyed every science course he could take, and his life at Penn had been marred only by a few required things, of which three stood out, viz., attendance at chapel a certain number of days per week ("This was not too bad, as it came early in the day and lasted ten or fifteen minutes"); a course in English composition which included the writing of essays ("Little did I realize how important this course was, but at the time it was a nuisance"); and a daily stint in the gymnasium ("Nothing can be more ridiculous than to go to a stuffy, smelly dressing room, put on some dirty, smelly gym clothes, then ascend to a large bare hard-floored room, not even well ventilated itself, and push up dumbbells at the behest of an instructor, followed by a run around an indoor track. . . . I was fundamentally an outdoors man who spent long hours tramping through woods and over hills").

In the fall of 1909 he found graduate work at Columbia University "really superb as compared with the undergraduate approach. One was free within certain limits to take anything one desired and to come and go at will. There was no compulsory chapel to attend, no English composition to write, or required exercise in a gymnasium. Curiously enough I actually spent much more time in the gymnasium at Columbia than I ever did at Penn. Since it was not so easy to reach the countryside from New York City as it was from Germantown, I felt the need of exercise. The Columbia gym had good handball courts and every day Professor Thomas Hunt Morgan, under whom I was working for a Ph.D. degree, some fellow students, and I played handball from 5 to 6 P.M. If the gymnasium smelt, I do not recall it, but I can assure any of those who tend to doubt, that a fast game of handball is a real workout, more than the equivalent of pushing dumbbells into the air all day long.

"These days at Columbia were really great, true examples of liberté, égalité, and fraternité. That is what graduate work should be. . . . Although Professor Morgan was nominally in charge of my thesis, I selected my own subject: 'The Permeability of Cells,' a field quite out of Morgan's interest. At that time he had just become involved with the heredity of the fruit-fly, *Drosophila,* his greatest work, and he made no objection to my selection of my own subject. His interests were so broad that he felt all subjects were worth pursuing. He himself had so many interests during his career.

"Morgan's lectures were sometimes supplemented by laboratory experiments or demonstrations. . . . I recall that one day we had a tubful of frogs for experiments on behavior and reaction to light. These frogs were supposed to do something in relation to the direction of a light beam, but I noticed that on this day all the frogs were very recalcitrant. When placed in the beam they either did not move, or if prodded, jumped in the wrong direction. I decided that study of amimal behavior was one involving too many unknown variables, not the subject for me; that I had better stick to the single cell, which is complicated enough, but cannot compare with an adult vertebrate animal."

Although Harvey took no botany courses at Columbia, he took practically all the courses offered in zoology, including the Invertebrate Zoology and Cytology courses of E. B. Wilson. For physiology and biochemistry he had to go to the College of Physicians and Surgeons, where he also worked on a minor research problem dealing with the phenomenon of treppe in muscle tissue.

During his two years of graduate school the summers (1910, 1911) were again spent first at Tortugas and then at Woods Hole, and Harvey's research on permeability was getting under way in earnest, though this period was still primarily one of learning, of "tooling up" for the prolific work he was to turn out beginning shortly thereafter. Alfred G. Mayor, who was soon to move to Princeton, was instrumental in recommending Harvey to the appointment of Instructor in the expanding Department of Biology under Conklin.

When Harvey came to Princeton in the fall of 1911, he found the small, sedate college town and relaxed atmosphere of the institution not altogether to his liking; he missed his companions in New York and the opportunities for recreation at operas, concerts, plays, good restaurants, etc., and he was lonely. Yet he was "determined to stick it out" despite these circumstances, as well as the facts that at the time Princeton was fundamentally concerned with the humanities, in which he was not particularly interested, and that scientific studies were on a small scale in comparison to his accustomed environment. A group of other young men, however, were newly arrived on the campus, to implement the preceptorial teaching system inaugurated a short time earlier by Woodrow Wilson before he resigned the presidency of the college to become governor of New Jersey. The young preceptors, representing various disciplines in the humanities, formed a Bachelors Club, chiefly as a dining place, and Harvey joined at the instigation of his philosopher friend, Ned Spaulding, with whom he had played tennis at Woods Hole. He thus became acquainted with broader aspects of human knowledge and culture. Among other things, he participated in group discussions of Henri Bergson and *L'Évolution Créatrice,* though he quickly concluded that "the philosophical approach was not definite enough to interest me and I withdrew as soon as I could find a good excuse." Instead, he attended numerous evening lectures, "on subjects I would never have thought of listening to at Pennsylvania or Colum bia," where all his time had been engaged in matters scientifi Moreover, he soon found that "the part of my education whic previously went in one ear and out the other was beginning t tarry a bit." There is little doubt that these diversions influence his scholarship in later years, as displayed, for example, in a outstanding appreciation of literature and history which per vaded his nearly 700-page monograph, *A History of Lumines* *cence from Earliest Times until 1900,* published in 1957, and his desire in retirement to write a booklet on the glowworm and firefly in history and literature, a projected work which unfortunately he did not live to complete.

Harvey's first untoward reactions in his initial appointment changed to a growing contentment. "Princeton University gradually developed its scientific departments and now ranks with the foremost in science studies. After a few years I became so loyal a Princetonian that no offer could have enticed me away, and I came to regard the town as the ideal place to live." In fact, it was not very long after his arrival that he was aware that "Princeton was beginning to entangle me with its charm. . . . Everything is in keeping with everything else. Nothing jars or jolts." Eventually he came to feel that "it is practically an emotional experience to walk around the campus and admire the flowering shrubs, so tastefully planted, to note the vines on the dormitories, and the lovely vistas, and the detail of carving on the buildings. How lucky I have been to live in such a place and yet to have New York and Philadelphia only one hour distant by train, while Washington and Boston can be reached in a few more hours."

In his long professional career, bioluminescence in all its aspects was the subject closest to his heart. Although he records that his interest in this field of inquiry was aroused while he was on the expedition with Alfred G. Mayor in 1913, he does not mention any particular incident or type of organism that sparked such consuming dedication to this field; perhaps it was a spectacular "phosphorescence" of the sea, of a kind he had observed earlier, or perhaps it was various luminescent representatives of the new marine life he encountered, and undoubtedly collected, there. It was impractical to bring such organisms back to his own laboratory; indeed, the source of light, when emanating from microscopic forms such as dinoflagellate protozoa, is often hard to identify with certainty, and it is difficult either to keep these as well as larger forms alive or to preserve the activity of their luminescence system in a dried condition. The small ostracod crustacean, *Cypridina hilgendorfii,* which he studied in 1916 at the Misaki laboratory in Japan, proved to be exceptional in that, when the organisms are properly dried soon after collecting, the luminescence system springs into brilliant activity on moistening with water, even after years of storage in a desiccated state. Partly for this reason, as well as usefulness of the system in experiments on kinetics of light emission, the influence of various factors thereon, the ease of separating the two organic components, i.e., the substrate "luciferin" and enzyme "luciferase," needed for a light-emitting reaction, and the sheer fascination of seeing the entrancing blue light produced on mixing aqueous solutions containing these components plus molecular oxygen, Harvey long maintained the view that "the *Cypridina* material has turned out to be by far the best for biochemical investigation of luminescence." Nobody knows how many kilograms of dried *Cypridina* were shipped, over the next forty years, from Japan to Princeton for his studies.

From a chemical point of view, however, this material turned out to present some frustrating difficulties, e.g., the luciferin is unstable in solution with oxygen, and it occurs in infinitesimal amounts, recently estimated as averaging about one microgram per organism at best, along with numerous unknown substances inert in luminescence but having similar gross properties of solubility and the like. Thus despite the assistance of able bio- and organic chemists who at one time or another were enlisted as Research Associates (among others, Rubert Anderson, Aurin Chase, Howard Mason, and Fred Tsuji), efforts to obtain pure luciferin, necessary to learn the chemical structure, were unsuccessful. Procedures were developed, however, by which the luciferin could be concentrated several thousandfold. These procedures were used, in part, when the crystalline product was finally obtained, concentrated some forty thousandfold as compared with the starting material, by O. Shimomura *et al.* in Japan (1957). Moreover, the kinetic studies of the unpurified system, begun by Harvey's first graduate student for the Ph.D. degree, W. R. Amberson, and later pursued by others with the partially purified system in Harvey's laboratory, established among other things that the brightness of luminescence provided a unique indicator of reaction velocity of the enzyme system involved. These results provided the basis for using bioluminescence as a "tool" for investigating the action of certain factors controlling enzyme activity in general, culminating in a rational theory for quantitative interrelations concerning the influence of temperature, hydrostatic pressure, narcotics, etc., on various biological processes *in vitro* as well as *in vivo,* largely through intensive studies of bacterial luminescence and other phenomena by H. Eyring, F. H. Johnson, and their associates at Princeton and elsewhere. This later work actually originated in collaboration with D. E. Brown and D. A. Marsland, who by 1940 had already laid a more empirical framework for the theory through a series of studies on the influence of increased pressure on muscle contraction, protoplasmic movement, viscosity, etc.

Purification of the enzyme luciferase, component of the *Cypridina* material, was never a major objective in Harvey's biochemical studies of this system. He did, however, obtain considerable evidence concerning its properties in unpurified or partially purified preparations, and his associate A. M. Chase succeeded in determining, with remarkable accuracy by indirect methods, quantitative values for its sedimentation constant, diffusion constant, molecular weight, Michaelis-Menton constant of the reaction with luciferin, etc. Harvey would have been gratified, had he lived, to witness (1962) the essentially complete purification of luciferase and the direct determination of its major properties, independently by O. Shimomura and F. H. Johnson in Princeton and by his former Research Associate, F. I. Tsuji, at Pittsburgh.

Prior to Harvey's work on *Cypridina,* only two examples of a "luciferin-luciferase reaction" had been known, and the only additional requirement to these components for light emission in aqueous solutions appeared to be oxygen. Dubois had introduced the terms "luciférine" and "luciférase" for the active principles which he separated in hot-water and cold-water extracts, respectively, of the West Indian elaterid beetle *Pyrophorus* (1885) and the boring clam *Pholas* (1887). Harvey's initial studies of *Cypridina* touched off a systematic, lifelong search for fundamentally the same type of system in virtually every kind of luminescent organism he could obtain, testing for the presence of a luciferin and luciferase in extracts prepared according to Dubois's method and in other ways. He also tested for the requirement of oxygen for luminescence of numerous organisms, finding exceptions only among certain protozoa, jellyfish, and comb-jellies (ctenophores), and he always tested for the specificity of the demonstrated or presumed enzyme-substrate systems involved, finding luminescent "cross-reactions" only among fairly closely related organisms, such as two genera of ostracod crustaceans (*Cypridina* and *Pyrocypris*), and among different families of fireflies; even today, only one example has been found of luminescent cross-reactions between the luciferins and luciferases of distantly related organisms, viz., of certain fish and *Cypridina.* When the requirement of adenosine triphosphate (ATP) as a cofactor in firefly luminescence was discovered in 1947 by W. D. McElroy, who had taken his Ph.D. degree under Harvey a few years earlier, Harvey tested, or arranged to test in collaboration with his colleague

Y. Haneda in Japan, for a possible role of ATP in the luminescence of a wide variety of organisms, with results indicating that this cofactor is significant only in the firefly.

Despite Harvey's determined and often ingenious efforts, however, relatively few types of luminescent organisms yielded a luciferin-luciferase reaction. Between about 1916 and 1931, his search revealed this reaction in only four types, viz., ostracod crustacea, American and Japanese fireflies, the marine "fireworm" *Odontosyllis,* and the deep-sea shrimp *Systellaspis.* Moreover, from then to the present time, only a few more types have been added to the list. Except in one instance, the newer types were discovered by Harvey's students, his students' students, or their associates. The first system in which the diffusible factors involved in the light-emitting reaction were chemically identified was that of luminous bacteria, which B. L. Strehler succeeded in extracting in 1953. When reduced flavine mononucleotide plus a long-chain aliphatic aldehyde were shown to be the minimal organic components needed for luminescence with bacterial extracts (Strehler, Harvey, Chang, and Cormier, 1954), Harvey remarked, "It is a great satisfaction to realize that Dr. McElroy took his Ph.D. with me at Princeton in 1943 and Dr. Strehler took a Ph.D. with Dr. McElroy at Johns Hopkins in 1952, so that I now feel decidedly like a grandfather of luminescence research."

For a full decade after 1916 Harvey concentrated the greater part of his research efforts on biological and chemical luminescence. He returned to Japan again in 1917 to study *Cypridina,* and worked on other forms in the Dutch East Indies in 1919, at Bermuda in 1921, at Naples and Sicily in 1925, and from time to time for years thereafter at various places in the Carribean and Central America during Christmas vacations. During the academic year, unless he had leave of absence for travel and research, he studied luminous bacteria, worked with his store of dried *Cypridina,* and investigated various aspects of chemiluminescence and other phenomena of "cold light." As a result he accumulated and published an immense amount of data pertaining to bioluminescence. Some papers were published in a volume collected under the auspices of a subcommittee on Chemiluminescence of which he was Chairman, and published under the title *Chemiluminescence* by the National Research Council in its Bulletin series. In fact, from 1916 through 1927 he was the single author of more than fifty technical publications on luminescence, as well as his first book (*The Nature of Animal Light,* 1920), some semipopular articles, and a few papers on other subjects.

His early experiments had resulted in some misleading evidence concerning the nature of bioluminescent systems in general, and prompted an oversimplified, optimistic view, which he expressed, however, along with a due note of caution and some prophetic perspicacity. Dubois's work had long remained buried in the scientific literature, without receiving the attention it deserved. Harvey confirmed Dubois's finding of a luciferin and luciferase in *Pyrophorus* and *Pholas,* and extended such results by discovering what appeared to be corresponding systems in fireflies. In 1916 he wrote that "bacteria also contain luciferin in very small amount and this can be precipitated with absolute alcohol and drying quickly. Such a dry powder gives no light with water, but a faint light with the luciferase of the firefly. I have been unable to obtain luciferase from the bacteria." Because of the sensitivity of firefly extracts to ATP, discovered many years later by McElroy (who, with his student Strehler, turned it to practical advantage as a general test for ATP), Harvey's results with "bacterial luciferin" may well have been due to the presence of ATP. In 1916 Harvey was led to believe that "luciferin of one form will act with the luciferase of another, and *vice versa.* This is true of the two genera of eastern fireflies (*Photinus* and *Photuris*) and for the West Indian *Pyrophorus* (Elateridae) and *Photuris* or *Photinus* (Lampyridae). . . . Whether the luciferin and luciferase of all forms are identical is still an open question. We know of many organic substances such as oils, alcohols, lophin, etc., which will phosphoresce at relatively low temperatures with alkalies so that it would be by no means remarkable to find that the luciferin of different forms was different. I have this past winter discovered a luminous reaction which is remarkable in many ways and which closely parallels the method of light production in luminous forms. Pyrogallol will produce light with the vegetable oxidases (potato or turnip juice) if we add some hydrogen peroxide. As little as one part of pyrogallol in 254,000 parts water ($m/32{,}000$) will give perceptible light and $m/8{,}000$ a good light. . . . Mammalian blood may take the place of the oxidase of plant juices." It is interesting to note that a few years later (1923) Harvey estimated that one part of *Cypridina* luciferin in from 4 to 40 billion parts of water would give perceptible light with crude *Cypridina* luciferase, and when crystalline luciferin was eventually tested with essentially pure luciferase of this organism by Shimomura, Johnson, and Saiga in 1961, it was found that only one part of luciferin in 10^{11} of solvent, i.e., 2×10^{-11} molar luciferin, resulted in visible light. Purification of an active substance which is normally present in only minute amounts requires not only the most sophisticated of modern biochemical techniques but also enormous amounts of raw material, which are often hard to come by among luminescent organisms in particular; for example, vast hordes of fireflies were used in McElroy's crystallization and structural determinations of firefly luciferin (1956, 1961), and upwards of twenty thousand individually dissected jellyfish, aggregating well over a ton, were employed in the isolation by Shimomura and Johnson (1961, 1962) of the unusual, oxygen-independent, single organic component system of *Aequorea.* In retrospect, with the fragmentary information and inadequate methods available in 1916 (and for a long time thereafter), it seems altogether natural that Harvey was led to conclude that "in a general way, then, we may say that the problem of luminescence has been solved at least in its broad aspects. There still remain many details to be filled in, details which will take some time to complete. The exact chemical nature of luciferin is unknown, but the method of attack of the problem has been outlined and all that is necessary is a sufficient quantity of the luminescent material for the determination of its chemical nature. That it may be difficult to obtain enough for analysis is indicated by the luminescence of pyrogallol which takes place at the almost inconceivably small concentration of 1:254,000."

He soon modified these early views, however, as he probed deeper into the biochemical nature of the systems involved. Eventually, casting a latent systematist's eye on the phylogenetic distribution of luminous organisms, he concluded that the property of light-emission had arisen sporadically and quite independently, probably as odd mutations which did not necessarily contribute to evolutionary survival value. He drew the analogy that it was as if someone had thrown a handful of sand at the phylogenetic tree, and wherever a grain of sand struck the name of a particular organism, that organism developed the property of luminescence. From the erratic distribution in nature (in some instances only one of two varieties of the same species is luminescent, as in the American and European varieties of the fungus *Panus stypticus*) and from differences in the emission spectrum and other characteristics of various systems, it was a logical step to conclude that the luciferin in each type of system was chemically different—a view that is still widely held, but one which reflects perhaps as much the persisting weight of his opinions as the available evidence, inasmuch as the chemical structure, in whole or in part, of only three or four types of "luciferin" is yet established. The most fully known system is that of the firefly, whose luciferase and luciferin were crystallized during Harvey's lifetime, and whose luciferin has since been synthesized, all by McElroy and his associates.

In addition to his prolific work on bioluminescence during this period (1916-1927), he maintained a full teaching schedule and he did not forsake his active interest in problems of permeability and the nerve impulse. For only a brief time in 1917 was his attention directed to other problems when, as part of the needs arising from World War I, he worked on the absorption of carbon monoxide and collaborated with the Navy Consulting Board on methods of illuminating the surface of the sea, as well as with the New Jersey Committee on Public Safety in connection with water reservoir contamination.

After this, to say the least, busy decade, he was, of course, well known and recognized as the world's authority on luminescence. In 1927, however, his interests became more diversified with the beginning of his lasting friendship with Alfred L. Loomis, who had just started a private laboratory for research on physical, chemical, and biological problems at Tuxedo Park, within easy commuting distance from Princeton by car. Among other distinguished scientists who worked at or visited this laboratory over a period of years was the physicist Dr. Robert Wood, who in the late 1920s perfected an apparatus for generating high-intensity supersonic sound waves. Harvey became interested in the biological effects of such a force and in the ensuing years published a number of papers on the action of supersonic waves on cells and tissues, foreshadowing the currently widespread, practically routine use of the supersonic method for disrupting cells in order to extract particulate fractions and enzymes, and for many other purposes.

With Mr. Loomis, Harvey soon turned to the development of the centrifuge microscope, which was brought into operation about 1930, and for which they received the John Price Wetherill Medal of the Franklin Institute in 1934. By means of this instrument it was possible to watch and photograph cells, under high magnification, as they revolved at 10,000 revolutions per minute, subjected to strong centrifugal force. Mrs. Harvey shared the use of the centrifuge microscope, which was perhaps the chief factor leading to her work with parthenogenetic merogones, known in newspaper parlance as "fatherless and motherless offspring." Thus, with this microscope, when sea urchin's eggs were suspended in an isopycnic medium, the internal components of the cells were observed to move under centrifugal force, oily constituents and the nucleus going to the centripetal end and the heavy pigment granules to the centrifugal end; the cell itself gradually drew out into a dumbbell, instead of its normally spherical shape, then separated into two halves. The enucleated halves, under subjection to certain physical stimuli, were found to undergo development without fertilization by spermatozoa, sometimes attaining as much as 500 cells, in the absence of the chromosomal hereditary material of either a father or mother, i.e., the phenomenon of artificial parthenogenetic merogony.

Shortly after he began working at the Loomis laboratory, Harvey's teaching responsibilities became somewhat reduced when his undergraduate course in general physiology was turned over (1928) to Philip Bard, though he maintained an interest in this course and wrote a new edition of the *Laboratory Directions* in collaboration with Bard's successor, A. K. Parpart, which was published in 1933. In that same year, Harvey was appointed Henry Fairfield Osborn Professor of Biology, on retirement of E. G. Conklin, which resulted in a further lessening of teaching obligations, although he continued to give his undergraduate course in biochemistry for another several years; he continued also to offer a graduate course in Physical Chemistry of the Cell as well as to supervise research of graduate students working toward their Ph.D. degrees.

On the whole, he thus had considerably more freedom to devote his energies to research and other activities, and he spent perhaps more time at the Loomis laboratory, where in 1935 he entered into a new field, that of electroencephalography which was just starting to receive widespread attention. In collaboration with Mr. Loomis and G. A. Hobart, the appropriate apparatus and equipment were assembled, including an enormous kymograph (eight feet long and four feet in circumference, surely the world's largest) with three writing pens to record electrical potentials from different regions of the brain over long periods of time, as during a night's sleep. The subject was placed on a cot in a soundproof room with various devices for causing auditory or other stimuli. An intercom system permitted communication with the adjoining room containing the control panels and kymograph. The resolve Harvey had made as a graduate student to "stick to the single cell, which is complicated enough," was overcome by the challenge of taking part in some of the pioneering research on electrical activity of the human brain, with particular reference to phenomena occurring during sleep, and through the next several years the team of Harvey, Loomis, and Hobart contributed a number of important papers on the subject. With the growth of knowledge and refinement of methods, electroencephalography has now become routine in certain areas of medical diagnosis and psychiatric or psychological research.

If at any period Harvey was more in the prime of life than at any other, it was perhaps between the late 1920s and the middle 1940s. In 1929 he was elected to membership in the American Philosophical Society, whose meetings he especially enjoyed and attended regularly thereafter; he took great pleasure in serving on the Society's Library Committee, the Meetings Committee, and the Publications Committee. In the same year he was elected to the Board of Trustees of the Marine Biological Laboratory at Woods Hole. In 1930 he became a Trustee of the Bermuda Biological Station, and also participated in the organization of an informal Cell Physiology Society which held meetings two or three times a year in New York, Philadelphia, or Princeton. "The discussions were a great success and the Society continued until 1937 when the meetings became so large as to be unwieldy and had to be abandoned." In 1931 he was appointed Managing Editor of the new *Journal of Cellular and Comparative Physiology* sponsored by the Wistar Institute of Anatomy and Biology in Philadelphia, and he retained this office until he resigned in 1939. At about this time he completed the manuscript of his second book on bioluminescence, *Living Light,* which was published in 1940. Beginning in the 1930s he also served as an editor of *The Biological Bulletin, Biological Abstracts,* the *Journal of Morphology and Physiology,* and the *Journal of Experimental Biology.* In 1934 he was elected to membership in the National Academy of Sciences. Throughout all this period he made numerous trips to Europe and elsewhere to attend international scientific congresses or other meetings, and to speak on such diverse topics as bio- and chemiluminescence, supersound waves, the centrifuge microscope, biological rhythmic processes, tension at the surface of living cells, and electrical potentials of the human brain.

In 1939 the long-smoldering international tensions in Europe erupted into World War II with all its catastrophic consequences and turbulent impact on the lives of countless individuals. Mr. Loomis foresaw that this country would soon be drawn into the conflict and he geared the research in his laboratory toward contributions of impelling strategic importance. The emphasis was changed from biophysics to radio communication, particularly in the range of ultra short waves, leading to the development of radar. Although Harvey maintained contact with this laboratory and attended some momentous conferences there, it was not long before he became immersed in problems relating to aviation physiology and wound ballistics in Princeton. During the academic year 1940-1941, which witnessed the inexorable transition in research objectives, Harvey resisted a tempting offer to head a new Department of Biology and Biological Engineering at the Massachusetts Institute of Technology, but accepted a position as visiting lecturer, conducting a course in cell physiology and related subjects which involved his spending two days in Boston and Cambridge every week from October 1940 to May 1941. At the end of this academic year, Edmund Newton Harvey, Jr., was awarded the degree of Ph.D. in Chemistry at Princeton.

Realizing that research along the lines of his personal interests was now out for some years to come, Harvey prepared to concentrate his efforts on matters of urgency to the Army and the Navy. In 1942 he began work for the Committee on Medical Research of the Office of Scientific Research and Development. Practically all graduate work as such came to a halt, although the assistance of graduate students as well as of professional personnel was brought to bear on the war projects that were initiated. He was made a member of the Subcommittee on Decompression Sickness of the Committee on Aviation Medicine, and a member of the Conference on Missile Casualties of the Committee on Medical Research. In these roles he directed two chief research projects, one on the factors involved and theory pertaining to bubble formation within cells and tissues, and the other on wound ballistics to find out what happened when a high-velocity missile penetrated organs and tissues. The former project was intensively but quietly pursued; the latter unavoidably made itself evident in the laboratory to students and teaching staff alike, for it entailed firing a high-velocity missile at deeply anesthetized animals at any time of the day. Before each shot a warning bell was rung, and there was probably more than one example of conditioned reflexes acquired by persons who repeatedly heard the explosions. With the aid of suitable X-ray and photographic devices, high-speed movies were taken of the impact and progress of the missile through the tissues of the target. At frequent intervals Harvey traveled to Washington and reported the results of these projects in a total of over twenty-five papers. Some of the work remains unpublished except in the form of reports of the National Research Council, although other unclassified aspects were given in journal articles, open lectures, and eventually as chapters in books, the latest of which, on the mechanism of wounding, appeared in 1962.

The end of the war in August of 1945 brought an end to Harvey's strenuous military research, even though some tasks remained, including the organization of reports and publications. This period marked the beginning of a more relaxed outlook, with more time for pursuits of his own interest. It should be mentioned parenthetically that his second son, Richard Bennet Harvey, at the same age his father received a Ph.D. degree, was awarded the M. D. degree, and it was a source of much satisfaction for Harvey to know that all members of his immediate family—his wife, his two sons, and himself—were now holders of a doctorate.

With the accumulated store of experience in his recent fields of investigation and a renewed activity in his former ones, together with his well-earned reputation as a good speaker, his love of travel, and the burgeoning facilities for speedy travel by air, it was only natural to expect that he would soon again be off on lecture tours to distant lands. In the spring of 1946 he flew to Brazil and gave a series of lectures on a variety of subjects at the Instituto de Biofísica in Rio de Janiero and at the university in São Paulo, in appreciation for which the Brazilian government bestowed on him the grade of Officer of the Ordem Nacional do Cruzeiro do Sul. The following winter he was appointed a delegate of the National Academy of Sciences to the Indian Science Congress and flew, with a brief stopover in London, to Karachi and Delhi. He traveled widely during his trips both to Brazil and to India. The following summer he attended the Cytology Congress in Stockholm and was elected Vice-President of the new International Society for Cell Biology.

Awards, honors, invitations, and appointments continued to mount. The award he appreciated most was the Rumford Medal for 1947 for his work on bioluminescence, conferred when he became a member of the American Academy of Arts Sciences in 1948. In the same year he received the Certificate of Merit from the President of the United States in recognition of his services to the armed forces during World War II. He became a member of the NRC Committee on Growth, the project leader of a sizable grant from the American Cancer Society to the Biology Department in Princeton, and a member of the Advisory Board of the Brookhaven National Laboratory on Long Island.

The next year he toured Switzerland under the auspices of the American-Swiss Foundation for Scientific Exchange and lectured on various subjects in Zurich, Basel, Bern, and Geneva, returning via Stockholm where he lectured at the Wenner-Gren Institute. In 1950 he gave an address at the dedication of the Jenkins Laboratory for Biophysics at The Johns Hopkins University and received the honorary degree of Sc.D. on that occasion.

At this time Harvey was about to enter upon his fortieth year on the faculty of Princeton. Members of the staff of the Biology Department concurred in a desire to honor him locally at a dinner. He was presented with a large scroll expressing their sentiments, lettered in Latin and decorated with figures, in fluorescent colors, of luminescent organisms he had studied. The scroll was illuminated with long wavelength ultraviolet light from a special fixture attached to the frame. To Harvey this informal gesture of appreciation from his friends and immediate associates was especially gratifying and enjoyable. Since the Latin text is susceptible of different versions in retranslation, the original English version is given below. The tribute set forth in this testimony by fellow members of the Department briefly summarizes the solid foundation for the esteem in which he was so widely held.

"The members of the staff of the Department of Biology, Princeton University, in honor of our most illustrious and highly esteemed colleague, Edmund Newton Harvey, Sc.B., Ph.D., Sc.D., N.A., natural philosopher, inquiring scientist, inspiring teacher, wise administrator, traveler abroad, promoter of knowledge, and congenial friend, on completion of forty years of zealous work and distinguished contributions in the interests of Princeton, of the nation, of science, and of students, and on completion of four decades of perspicacious investigations of physiological phenomena in general and of the mysteries of luminescence in chemistry and in life in particular, this dinner is respectfully and affectionately dedicated, on this thirteenth day of November, in the year of our Lord, 1951."

Although there was no real slowing down of his activities, he was now devoting a larger share of his time to writing, with the tedious, exacting library research it entailed. His third book, entitled *Bioluminescence,* was published in 1952, and his fourth, *A History of Luminescence,* in 1957, in the year following the publication of Mrs. Harvey's scholarly monograph on her lifetime interest, the sea urchin, and the award of an honorary D.Sc. degree by her alma mater, Goucher College. In addition to his writing, he continued to accept offices of prestige and responsibility, such as the presidency of the American Society of Zoologists, in which capacity he delivered the presidential address at the Boston meetings in 1953 and presided over a symposium he organized on "Bioluminescence as a Tool in the Study of Cell Processes." He also continued to travel and attend conferences, including one on luminescence sponsored by the National Research Council Committee on Photobiology with the support of the National Science Foundation and held at Asilomar, California, in 1954. The following year he had his "last fling" at war science when he attended a Conference on Underwater Physiology, sponsored by the National Research Council Committee on Undersea Warfare, and spoke on bubble formation, illustrating his presentation with high-speed movies taken in 1943. In the summer of his retirement in 1956 he gave the presidential address of the American Society of Naturalists, which was meeting with the American Institute of Biological Sciences, on the subject of "Evolution and Bioluminescence." In 1959 he was awarded the honorary degree of LL.D. by Temple University.

His last graduate course on Cell Physiology was given in somewhat unusual form in the spring of 1956. It consisted of a series of lectures on the various fields in which he had been particularly interested over the years. He listed them as follows: "(1) Cell stimulation phenomena, i.e., excitation; (2) Nature of the nerve impulse; (3) Rhythmic phenomena and temperature effects; (4) Brain potentials; (5) The centrifuge in biology; (6) Tension at and nature of the cell surface; (7) Bubble formation and decompression sickness; (8) Photochemistry and light measurement; (9) Bioluminescence; (10) Wound ballistics; (11) High frequency sound waves and their biological effects." After the final lecture in this course, he wrote in his notes: "For all practical purposes my status is now emeritus except that I will be in charge of a research project for another year and will always retain an interest in the advancing front of scientific discovery, with more time to spend on matters not immediately concerned with cell physiology."

At the end of the month, he was again honored by his departmental colleagues at a party and dinner which he profoundly appreciated and enjoyed. "It was held on May 31, 1956, very informal and jolly (with red Pino noire), and gave me an opportunity to compare earlier days in Princeton with the present University. Also to say that during my forty-five years on the faculty, no one ever interfered in any way with my teaching or research; no one attempted to direct my research or even to suggest that certain lines of inquiry might be of interest to the University. At Princeton it has always been assumed that a faculty member, no matter how young, is capable of choosing his special field of interest and he is permitted to carry out his ideas to the best of his ability, surely a wise and praiseworthy policy. Under the presidencies of Hibben and Dodds, I have seen Princeton pass from the reputation of a nice country club to one of the highly regarded centers of learning in the U.S. and I am proud to have played even a small part in the change. . . . I only wish that I could call myself an alumnus in fact as well as in feeling. At the dinner Ethel and I were presented with gold keys . . . making us members of an exclusive scientific fraternity of two. The E.N.H. key had figures of luminous organisms, bacteria and *Cypridina,* engraved on it, while the E.B.H. key had of course an *Arabacia* and its developmental stages."

During the remaining three years of his life he was unpressed but busy and to all appearances he enjoyed the increased freedom afforded by his status of Professor Emeritus. His major research activity continued in the field of bioluminescence; in fact, a notable number of his papers on this subject were published after he retired, and six more which were still in press appeared posthumously. When he died, with merciful suddenness, on the morning of July 21, 1959, at his home in Woods Hole, science lost a distinguished biologist, Princeton lost a scholarly teacher, and a multitude of associates lost a genial friend.

GENEALOGY

Nimrod Harvey, b. about 1700	Richard Newton, b. about 1601, at Sudbury, England; came to and helped found Sudbury, Mass., 1638; d. 1701
James Harvey, b. about 1730	Daniel Newton, b. 1655, at Sudbury, Mass.; d. 1739
	Samuel Newton, b. 1695, at Marlborough, Mass.
Joseph H. Harvey, b. 1760	Lemuel Newton, b. 1718, at Marlborough, Mass.; d. 1793 (soldier of the revolution)
David Harvey, b. 1791; came to the U.S. in 1808 from Omagh, County Tyrone, Ireland; of Scotch-Irish descent	Edmund Newton, b. 1751, at Southborough, Mass.; d. 1816 (soldier of the revolution)
	Thomas Newton, b. 1783, at Philipston, Mass.; d. 1848
	Edmund Newton, b. 1816, at Philipston, Mass.
William Harvey, b. Feb. 12, 1835, in Philadelphia; d. 1893	Althea Ann Newton, b. 1846, at Philipston, Mass.; d. 1926

Edmund Newton Harvey, b. Nov. 25, 1887; d. July 21, 1959; married, March 12, 1916: Ethel Nicholson Browne

Edmund Newton Harvey, Jr., b. Dec. 16, 1916; married, June 15, 1946: Jeanette Hickman	Richard Bennet Harvey, b. March 5, 1922; married, Nov. 9, 1946: Janet Miller
Virginia Nicholson Harvey, b. Jan. 2, 1948; Sara Newton Harvey, b. June 4, 1949; Christopher Neale Harvey, b. March 23, 1955	Robert Brooke Harvey, b. May 26, 1949; Pamela Day Harvey, b. March 22, 1951; Philip Nicholson Harvey, b. Nov. 29, 1952

SELECTED CHRONOLOGY OF SCIENTIFIC MEMBERSHIPS, APPOINTMENTS, POSITIONS, AND ACADEMIC DEGREES

1905 Academy of Natural Sciences, Philadelphia; member of Entomological Section (to 1909)
1907 National Geographic Society, member
1909 B.S., University of Pennsylvania
Society of the Sigma Xi, University of Pennsylvania Chapter
Collector, Tortugas Laboratory, Carnegie Institution of Washington
Scholarship, Columbia University Graduate School
1910 American Association for the Advancement of Science, member
Collector, Tortugas Laboratory, Carnegie Institution of Washington
Fellowship, Columbia University Graduate School
1911 Ph.D., Columbia University
Instructor in Biology, Princeton University
Member of the Corporation of the Marine Biological Laboratory, Woods Hole
1913 American Society of Zoologists, member
American Society of Naturalists, member
Expedition to the Great Barrier Reef of Australia, member
1914 American Physiological Society, member
International Zeitschrift für Physikalisch-chemische Biologie, Mitarbeiter
1915 Assistant Professor of Biology, Princeton University
1916 American Society of Biological Chemists, member
1917 Research Associate, Carnegie Institution of Washington
1919 Professor of Biology, Princeton University
Society for Experimental Biology and Medicine, member
Research Associate, Carnegie Institution of Washington
1920 American Association of University Professors, member
1921 Fellow, American Association for the Advancement of Science
1924 Visiting Associate, Nela Laboratories of the General Electric Company
1925 American Chemical Society, member
National Research Council Committee on Chemiluminescence, Chairman

1929 American Philosophical Society, member
Trustee, Marine Biological Laboratory, Woods Hole
1930 Editor, *Journal of Experimental Biology* (to 1934)
Editor, *Journal of Morphology and Physiology* (to 1932)
Editor, *Biological Bulletin* (to 1953)
Section Editor, *Biological Abstracts* (to 1953)
Trustee, Bermuda Biological Station (to 1952)
Botanical Society of America, Physiology Section, member
1932 Managing Editor, *Journal of Cellular and Comparative Physiology* (to 1939)
Charter member, Princeton Chapter, Society of the Sigma Xi
1933 Henry Fairfield Osborn Professor of Biology, Princeton University
Research Committee, Princeton University
1934 National Academy of Sciences, member
John Price Wetherill Medalist of the Franklin Institute
1938 President, Princeton Chapter, Society of the Sigma Xi
Sigma Xi National Lecturer
1939 Society for Growth and Development, member
1940 Visiting Lecturer, Massachusetts Institute of Technology
1942 Editor, *Review of Scientific Instruments* (to 1945)
Vice-President, Marine Biological Laboratory, Woods Hole
Advisory Committee, Department of Zoology, Columbia University, member
National Research Council, Division of Physics (to 1945)
1943 Intermission speaker, broadcast of New York Philharmonic Concert
NRC Committee on Aviation Medicine, Subcommittee on Decompression Sickness (to 1946), acting for the Committee on Medical Research of the Office of Scientific Research and Development (OSRD)
OSRD Committee on Medical Research, Subcommittee on Missile Casualties (to 1946)
1944 NRC Conference on Wound Ballistics (to 1946), acting for the OSRD Committee on Medical Research
Fellow, New York Academy of Sciences
Harvey Lecturer, New York Academy of Medicine

1945 New York Zoological Society, member
1946 Visiting Lecturer, Instituto Biofísica, Rio de Janiero, Brazil
Officer of the Ordem Nacional do Cruzeiro do Sul, Brazil
Visiting Lecturer, Graduate School, Ohio State University
Charter member, Society of General Physiologists
Advisory Board, Survey of Biological Progress
1947 Chairman of Biology Section, National Research Council Committee on Growth (to 1950)
American Academy of Arts and Sciences, Rumford medalist and member
Delegate of the National Academy of Sciences to the India Science Congress
Vice-President (to 1950) and charter member, International Society for Cell Biology
Advisory Board, Brookhaven National Laboratory
1948 Certificate of Merit from the President of the United States
1949 Lecturer, American-Swiss Foundation for Scientific Exchange
Advisory Board, *Experimental Cell Research*
Advisory Committee, Biology Department, Massachusetts Institute of Technology
1950 Honorary Sc.D., The Johns Hopkins University
President, International Society of Cell Biology
Socio corrispondente nella Classe di Scienze, Sezione di Scienze Naturali, Istituto Lombardo di Scienze e Lettere
1951 Editor, *Archives of Biochemistry and Biophysics*
Charter member, Radiation Research Society
Recipient of Testimonial Scroll, Biology Department, Princeton University
1952 President, American Society of Zoologists
1953 Library Committee, American Philosophical Society
1955 Program Committee, American Philosophical Society
1956 President, American Society of Naturalists
Henry Fairfield Osborn Professor Emeritus of Biology, Princeton University
1959 Honorary LL.D., Temple University

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KEY TO ABBREVIATIONS

Am. J. Physiol. = American Journal of Physiology
Am. Scientist = American Scientist
Arch. Biochem. Biophys. = Archives of Biochemistry and Biophysics
Biochem. Bull. = Biochemical Bulletin
Biol. Bull. = Biological Bulletin
Carnegie Inst. Wash., Dept. Marine Biol., Papers = Carnegie Institution of Washington, Department of Marine Biology, Papers
Carnegie Inst. Wash. Year Book = Carnegie Institution of Washington Year Book
J. Am. Chem. Soc. = Journal of the American Chemical Society
J. Cellular Comp. Physiol. = Journal of Cellular and Comparative Physiology
J. Gen. Physiol. = Journal of General Physiology
J. Neurophysiol. = Journal of Neurophysiology
Proc. Am. Phil. Soc. = Proceedings of the American Philosophical Society
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society for Experimental Biology and Medicine
Sci. Am. = Scientific American
Sci. Monthly = Scientific Monthly

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1931

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