NATIONAL ACADEMY OF SCIENCES

WINTHROP J. V. OSTERHOUT

1871—1964

A Biographical Memoir by

L. R. BLINKS

Any opinions expressed in this memoir are those of the author(s) and do not necessarily reflect the views of the National Academy of Sciences.

Biographical Memoir

WINTHROP JOHN VANLEUVEN OSTERHOUT

August 2, 1871–April 9, 1964

BY L. R. BLINKS

WINTHROP JOHN VANLEUVEN OSTERHOUT was born in Brooklyn, New York, on August 2, 1871, a little over a century ago. He died in New York, April 9, 1964. Elected to the National Academy of Sciences in 1919, he lived to be one of its older members (aged ninety-two). He greatly influenced the course of biology in the United States, as it turned from a largely descriptive into an experimental and analytical science. He was one of the founders of the new discipline of general physiology, through his own work and through his editorship of the *Journal of General Physiology,* which he founded, with Jacques Loeb, in 1918. He remained an editor for over forty-five years, and trained many students who contributed to general physiology.

Winthrop Osterhout was the son of the Reverend John Vanleuven Osterhout and Annie Loranthe Beman Osterhout, the only child of Mr. and Mrs. R. Beman of Brooklyn. The mother's family were English; she lived in Baltimore before her marriage. The Osterhout family were Dutch, having come, as the name implies, from the town of Oosterhout (East Wood) south of the Rhine delta near Breda in the North Brabant province of the Netherlands. Jan Jansen van Osterhout and his wife, Annetje Gielis, came to New Amsterdam (later New York) before 1653, and lived first in Brooklyn; they moved up the Hudson, settling near Kingston. Later many family members lived in the vicinity of Ellensville, in Ulster County, and Winthrop's uncle William was a tanner in Tannersville, in the Catskills.

There seem to be no New England ancestors to account for the distinguished name of Winthrop, which may have been given for some good friend. At the time of Winthrop's birth his father was a Baptist minister in Webster, Massachusetts, his congregation consisting largely of working people of very small means. John Osterhout was an idealist who preferred to minister to poor people, rather than seek a position at a wealthier church. When Winthrop's mother and infant sister died of typhoid fever in 1873, the boy was left without a nurse. At first his father tried to care for the boy himself, and wrote that "Winnie is a good little traveller," when he took his son along wherever he went to preach. However, this arrangement proved too difficult, and young Winthrop was sent to live with his grandmother in Baltimore. This was apparently a happy time, since Grandmother was easygoing and gave him much freedom to play with boys of his own age on the street.

Meanwhile the elder Osterhout had remarried, but his second wife died very soon, and Winthrop never knew her. Finally, when he was eight years old, Winthrop moved to Providence, Rhode Island, where his father had again remarried; here he grew up under the care of his stepmother, who was good to him, although never very close; she was a somewhat formal person who always addressed her husband as Mr. Osterhout, or "Mr. O." However, Winthrop knew her as Mother; she lived into the third decade of the next century. The parents had bicycles and took trips on them, but the boy was not included, and in general did not enjoy athletics. He did not play games, not even tennis, and apparently did not have any close boyhood friends that he could remember. In later life his chief recreation was walking and rowing.

His father's church in Providence was also a poor one, and the family never enjoyed affluence. Winthrop attended Bridgham Grammar School and Providence High School; when he was ten years old he got a job as errand boy in a bookstore, where he had a chance to get acquainted with books. His employer liked him and allowed him to read; from then on most of his leisure time was spent in reading. Finally, when he entered Brown University in 1889, he was entranced by the collection at the library. He at least glanced into every book on the shelves to see whether the contents interested him—a feat possible in 1890 but scarcely in any present university library! He was interested mainly in literature, and was elected class poet; he probably would have become a teacher of literature had not one of those chance happenings deflected him to science. In his junior year he met Professor H. C. Bumpus, who had recently come to Brown from Olivet (a small Congregational college in Michigan that had a remarkable succession of good biologists on its staff). Bumpus urged Osterhout to attend the botany course at nearby Woods Hole, in the summer of 1892; there the famous Marine Biological Laboratory, then only four years old, was just getting established. Here were such biologists as T. H. Morgan, E. G. Conklin, Frank Lillie, and Jacques Loeb, who later became a very close friend. The teacher of the botany course was W. A. Setchell, a recent Ph.D. of W. G. Farlow's at Harvard and then Instructor at Yale.

Osterhout and Setchell often went on collecting expeditions. Here began Osterhout's acquaintance with marine and freshwater algae—the organisms he was to exploit so successfully in later research. One day he actually found *Nitella* in Nobska Pond, though it was thirty years before its physiological advantages were recognized. (Fifty years later Osterhout was to write Setchell's biography for the American Philosophical Society.)

Osterhout made such an impression on Setchell that the latter invited him to assist in the course next summer, which he did, immediately after graduating. Now he was given the opportunity to do independent research, and discovered an interesting phenomenon in *Rhabdonia tenera* (now known as *Agardhiella*): four spores, each capable of forming a new plant, could also combine to form a single plant. This was the subject of Osterhout's first paper, in the *Annals of Botany.* He was also intrigued by plants living in brackish water, and tried some experiments that were the beginning of his later work on osmotic pressure and salt effects in algae.

Osterhout returned to Brown in the fall of 1893 as Instructor in Botany, remaining for two years while he studied for the M.A., which he took in 1894. He was able to spend the next year in Germany, where so many young American scientists then went for their graduate training. No doubt Setchell encouraged this move; in any case the young Osterhout chose Bonn, where Eduard Strasburger was then at the height of his fame as a plant cytologist. The great professor was very kind and helpful, and the atmosphere of the laboratory was congenial; Strasburger made the students his friends. Here Osterhout met other young Americans: R. A. Harper, who took his Ph.D. at Bonn that year and later taught at Wisconsin and Columbia; and David Fairchild, who became the famous "plant hunter" for the Bureau of Plant Introduction. (Curiously, in view of Osterhout's later utilization of *Valonia,* Fairchild went on from Bonn to Naples, where he investigated the cytology of that genus.)

At Bonn Osterhout worked on the cytology and reproduction of the freshwater red alga *Batrachospermum.* It was necessary to collect the plants at all hours of the day and night to find the proper stages—which led to some interesting conversations (in German) with farm dogs and also with the *Polizei,* who were suspicious of the collecting equipment: dark lantern and *gummischuhen!* These experiences no doubt contributed to Osterhout's good command of the German language, which he read easily and spoke well. He published several papers in German periodicals.

When the time came to return home in 1896, Osterhout had a position awaiting again at Brown, but chose instead to move west, to the University of California, then only 28 years old. Setchell had preceded him to Berkeley as Professor of Botany, and he appointed Osterhout as instructor in his department. At this grade the young man remained for five years while he completed his dissertation on the reproduction of *Rhabdonia,* the alga on which he began work in Woods Hole. He was awarded the Ph.D. degree in 1899 and was married the same year to Anna Maria Landstrom, Winthrop's father coming out from Providence to perform the ceremony. A daughter, Anna (Mrs. Theodore Edison), was born in 1901 and another (Mrs. Olga Osterhout Sears) four years later. Their aid in the preparation of this memoir is gratefully acknowledged.

Osterhout was promoted to Assistant Professor of Botany in 1901 and to Associate Professor in 1907. The years at Berkeley were exciting and influential ones. The university, up to that time an isolated and small institution, was beginning to take on the stature of greatness that it later assumed, partly because of the rapid growth of California, partly because of the competition of its new neighbor at Stanford, but mostly because of its remarkable president, Benjamin Ide Wheeler (another graduate of Brown). In a day of famous leaders, Wheeler was a great builder and stimulator. One of his notable innovations was the bringing of great scholars from Europe for a year; some of these arrivals in science were Arrhenius from Sweden, de Vries from Holland, and Ostwald from Germany (whose name meant the same thing as Osterhout). There also came to Berkeley for a period of eight years the brilliant physiologist Jacques Loeb, who influenced Osterhout very greatly. There exists a photograph taken in 1905 showing de Vries beside an *Oenothera* plant in the botanic garden, flanked with the portly Arrhenius and the ascetic slight figure of E. W. Hilgard, with Loeb smiling beside them, and Osterhout (in "bowler" hat) in the back row.

It was a fruitful and stimulating society for a young scientist, and it is not surprising that Osterhout's thoughts began turning from cytology and morphology to physiology and physical chemistry. These were the days of Loeb's interest in artificial parthenogenesis (experiments on which were carried out in the Herzstein Laboratory near Monterey), and "salt effects" were at the center of the physiology of the day. Osterhout began looking at algae from this point of view, noticing a perfectly natural experiment. He observed the plants on the hulls of river steamers going daily from the salt water of San Francisco Bay to the mountain-fresh water of Sacramento. Those plants which survived could obviously tolerate wide ranges of salinity. He also looked into the necessity of calcium to balance sodium, both in algae and in the roots of higher plants; these observations were the subject of several short papers. In addition, he wrote two books. A remarkable one, entitled *Experiments with Plants,* described simple, ingenious class exercises which could be performed with seeds, corks, and lamp chimneys. There was even included a homemade balance, sensitive to one-tenth of a gram, made from umbrella ribs! While this book was scorned by sophisticated colleagues who remembered Pfeffer's laboratory, its exercises were characteristic of Osterhout's "make-do" methods, and the book was still in use twenty years later in his Harvard elementary class. I found it very useful when I began to teach in a poorly equipped laboratory (ironically that of one of the scorners noted above). Apparently others did also, for it was translated into Dutch within two years, and later into Russian (by none other than the distinguished plant physiologist, N. A. Maximov). It might still be useful in underdeveloped countries. It contained some illustrations from Luther Burbank, whom Osterhout knew.

The other book, written in collaboration with the famous agricultural and viticultural expert E. W. Hilgard, was entitled *Agriculture for Schools of the Pacific Slope.* While both books might be regarded as economic potboilers, they added greatly to the young botanist's reputation. At Berkeley, as his fame grew, Osterhout attracted increasing numbers of graduate students, among whom were A. A. Lawson, C. L. Williams, E. S. Byxbee, H. T. A. Hus, N. L. Gardner, and H. D. Densmore, the last a professor at Beloit College at the time of his work at Berkeley. All of these students worked on cytological problems: polar caps, spindle fibers, and the like. F. N. Magowan, however, studied the effects of salts on plants, reflecting Osterhout's own changing interests. Nathaniel L. Gardner, who was seven years older than Osterhout, became one of his most distinguished students, writing a large number of papers on Pacific Coast algae, many in collaboration with Osterhout's professor, Setchell. He and Osterhout went on collecting trips together—perhaps on the one from Monterey to Big Sur, aboard a very recalcitrant burro, which Osterhout recalled with amusement.

Berkeley had many charms—its genial climate, good times at the Bohemian Grove, friendship with colleagues, and the beginnings of the university's later greatness. But it was a long way from other centers; except at Stanford there was then little science west of Chicago, and the long trip east by train was wearisome and expensive. Osterhout had not visited Woods Hole for many years. Therefore it was not surprising that in 1909 when Harvard offered him an assistant professorship, he accepted, despite the step down in rank—and a "munificent" salary of $1500 per year (paid quarterly, moreover, which created financial problems on arrival in Cambridge). Loeb also left Berkeley the next year, to join the Rockefeller Institute for Medical Research in New York.

In Cambridge, Osterhout inherited the laboratories just vacated by G. L. Goodale—rooms in the "Agassiz Museum," that red-brick pile of New England mill architecture that still houses the Museum of Comparative Zoology, as well as the geological, anthropological, and some botanical collections, especially the "glass flowers" that attracted the tourists in flocks past Osterhout's office on the second floor. It is not surprising that later he carried on much of his research in a greenhouse in the Botanical Garden several blocks away. M. L. Fernald was in the Gray Herbarium; W. G. Farlow, Roland Thaxter, and E. C. Jeffrey in the Museum.

With such a collection of stars, life was not easy. Jeffrey in particular was soon in open enmity, even threatening to "shoot that damn Dutchman." However, there were many friendships as well, especially with George Howard Parker, the genial Professor of Zoology, who became probably Osterhout's best friend in Cambridge. With him, and those students who wished to attend, there were long walks on Sundays, often ending with a meal and red wine at the "Stella d'Italia" on the North Side of Boston. Osterhout became a member of two clubs, one consisting mostly of Harvard professors in Cambridge, the other (the Thursday Club) meeting in Boston and including prominent nonacademic people. President Lowell was always friendly. But still the salary remained low (Harvard then paying in the currency of prestige), and Osterhout had to eke out his earnings by teaching a course at Radcliffe as well as a Saturday morning extension course for teachers. He never owned an automobile, and he could be seen walking home to Buckingham Street in the evening, carrying a Harvard green baize bag full of papers and calculations, and lost in plans for the next day's experiments. About this time he taught himself mathematics, which now began to play an important part in his work.

Among his friends were the chemists G. P. Baxter, A. B. Lamb, and Theodore Richards, who was soon to be the first American to receive the Nobel Prize in chemistry. They appreciated his applications of chemistry to biology, and he established good "diplomatic relations" with them so that his students could quickly obtain advice in their work—an invaluable asset of being in a famous university.

In the summer of 1910 he returned to Woods Hole, where he worked almost every summer for the next dozen years. He was elected a trustee of the Marine Biological Laboratory in 1919, remaining on the board for thirty years. Now began a most fruitful period of research, when he employed a new organism for studying salt and other permeability effects, and a new technique (for biology) to measure them. The organism was the brown alga or kelp, *Laminaria;* the technique, electrical resistance of the tissue. The thin blade of the kelp was cut by a cork-borer into small disks and arranged in columns, like a pile of pennies, then inserted into a Kohlrausch bridge, such as was used for measuring the conductivity of electrolytes. The conductivity of the tissue was assumed to represent the permeability of its cells to the ions of the bathing solution. He was perhaps influenced in the choice of this technique by his friendship with Arrhenius, who had recently developed his theory of ionic dissociation. The current source was a tuning fork oscillator of 1000 Hertz, detected by a telephone. Of course, this circuit really measured *impedance,* but it was, because of the large number of cells in series, adequate for the purpose. His results were later confirmed with direct current resistance measurements by the writer.

Osterhout's procedure had the great advantage of giving quantitative measurements of changes in permeability from moment to moment, permitting the construction of time curves which could be used for calculation and prediction. It was found that the resistance remained high and constant in sea-water, for long periods. On the other hand, a single salt, such as NaCl of the same conductivity, produced an immediate fall of resistance; if the exposure was continued for some hours, the fall was all the way to that of a dead tissue, completely permeable. Conversely, the resistance recovered if seawater was restored before the resistance had fallen all the way to the dead value. Thus injury and recovery were shown quantitatively.

Some divalent ions such as Ca, on the other hand, caused a rise of resistance at first, even to 60 or 70 percent above normal, which would be maintained for some time before falling, eventually to the dead value. Again there was recovery if the tissue was restored to seawater soon enough. However, if a mixture of the two salts (e.g., 97.5 percent Na, 2.5 percent Ca) was applied, each injurious *alone,* the tissue remained undamaged, the resistance maintaining its normal value, neither rising nor falling for long periods. Obviously a *balanced solution* had been attained between two ions (each separately injurious), and the principle of salt antagonism beautifully and quantitatively demonstrated. Varying mixtures of these salts, as well as others, were studied, as were the effects of acid and alkaline seawater, anesthetics, surface active substances, etc. The method was employed as well by several of Osterhout's students, and a great number of papers described the results, at first largely in *Science,* then in other journals. These studies were summarized in a series of Lowell Lectures, given in Boston in 1922, and assembled in a book entitled *Injury, Recovery and Death in Relation to Conductivity and Permeability,* published in a new series, "Monographs on Experimental Biology," of which Osterhout was an editor, along with Jacques Loeb and T. H. Morgan. It was one of Osterhout's best books, carefully written and demonstrating his facility in mathematics; but the assumptions used, a series of consecutive reactions in which a hypothetical substance M is formed by the reaction $A \rightarrow M$, and decomposed by the reaction $M \rightarrow B$, controlled by Ca and Na, respectively, were not directly demonstrated. This was the culmination of the *Laminaria* work, other matters now beginning to occupy Osterhout's attention. Indeed, only four or five more papers on these topics were published in the new periodical founded by Loeb and Osterhout, the *Journal of General Physiology,* of which the first number appeared in September 1918. Osterhout remained an editor for forty-five years. The journal was the main place of publication for him and his students and collaborators thereafter.

Volume I, No. 1 of *J.G.P.* contained a description of a new method of measuring respiration and photosynthesis, namely by the color changes produced in pH indicators by the production or utilization of CO_2. The first article (written with A. R. C. Haas) utilized this principle to study the "induction period" of photosynthesis; the second described an apparatus to circulate air from reaction chamber to indicator by means of a rubber bulb, with a soda lime tube to absorb CO_2. This apparatus was run with a motor and was dubbed the "Mills of the Gods"; it was the basis of a number of dissertations by students. Students doing their doctoral work on this or other problems were (as far as I can ascertain) W. T. Bovie, G. B. Reed, A. R. C. Haas, S. C. Brooks, M. M. Brooks, O. L. Inman, G. B. Ray, F. G. Gustafson, W. O. Fenn, Oran L. Raber, S. F. Cook, C. J. Lyon, P. A. Davies, and L. R. Blinks. This seems a small list for sixteen years, but Ph.D. factories were smaller in those days. Some half dozen of these students predeceased Osterhout; others went on to productive careers, two becoming members of the National Academy of Sciences.

Osterhout was promoted in 1913 to the rank of Professor, at the age of forty-two, four years after his arrival in Cambridge. For much of his Harvard career he was in charge of the elementary botany course, which he enlivened with simple but dramatic experiments, many of which could be demonstrated in lectures. He was a polished, effective speaker, who enjoyed making startling statements, and was not above showmanship when it could illustrate a point. He had to do this, he later explained, to keep the interest of Harvard's gilded youth, some of whom even brought bulldogs to class and aimed at the

Gentleman's C, in the days before the "Intellectual Renaissance" on the Charles. (Among his advisees was Vincent Astor, who was always accompanied by a bodyguard!) His advanced lectures, on the other hand, were serious, carefully studied efforts, filled with the latest research results, often freshly published in the newest *J.G.P.* Although his courses in plant physiology continued to bear the Pfefferian rubrics "Assimilation and Respiration," or "Growth, Irritability, and Reproduction," they were actually more and more concerned with the newest theories of enzyme action and of cellular permeability—in other words, general physiology. Indeed, for a long time his classes were the only place in Harvard College where practical work in biochemistry could be studied. L. J. Henderson, who taught biological chemistry, offered no laboratory; Otto Folin was at the Medical School, many miles away in Boston. Osterhout's courses consequently attracted many able students, not only in botany, but from zoology, and from the Bussey Institution, a dozen miles away. Through much of his stay in Harvard, Osterhout was faithfully assisted by Lee Morrison, who also performed many of the *Laminaria* experiments, and was addressed by some students as "Professor Morrison."

Around 1921 the emphasis changed to study of large coenocytic algae, at first *Nitella* and *Chara,* from each cell of which a drop of vacuolar sap could be drained, either for analysis of the sap (which was found to be very different from the surrounding solution), to follow its changes on injury, or to study the penetration of new substances from outside. Osterhout's first paper on *Nitella* dealt with the rate of loss of chloride ions under injury (e.g., by chloroform), determining chloride in the sap by microtitration. He also measured the fall of electrical impedance of *Nitella* under injury, but the method (at 1000 cycles) was not capable of showing very great changes, on account of the cell's high capacitance. (Direct current was later employed by the writer, with much higher resistance values demonstrable.) Beginning in 1922, a start was made on bioelectric measurements with *Nitella,* under a Carnegie Institution grant, which enabled E. S. Harris to assemble electronic equipment and literally *make* a string galvanometer. The study of dye penetration into *Nitella* also began at this time, in collaboration with Marian Irwin, a recent Ph.D. student of G. H. Parker.

In 1923 work with giant marine algal cells began. Years earlier, at Osterhout's suggestion, R. P. Wodehouse, then a Harvard graduate student, had gone to Bermuda in 1916 and studied the vacuolar sap of *Valonia macrophysa.* This is a coenocytic alga, the large cells of which can each yield one ml or more of sap with a minimum of contamination by seawater. Wodehouse found potassium to be abundant, while sulfate was absent, in the sap. W. J. Crozier in 1919 found the pH of the sap to be about 6, while that of the seawater was 8.1 or so. Crozier had also sent to Osterhout a large volume of sap from *Valonia* for careful chemical analysis by L. M. van der Pyl in Baxter's laboratory at Harvard. The analysis confirmed Wodehouse's qualitative findings. K was found to be 40 times as concentrated in the sap as in seawater, while Na was one-fifth to one-sixth as concentrated: K was accumulated, Na was partially excluded. Cl was a little higher in the sap than in seawater, while SO_4 was excluded (as was Mg).

The stage was now set for the study of *Valonia* at its place of growth; it was necessary to go to Bermuda for this. A grant (not at all common in those days) was obtained from the Rockefeller Institute, a sabbatical leave was arranged for the first term of the college year, and in the summer of 1923 Osterhout took the *Fort Victoria* of the Furness line to Bermuda. His assistant was Mr. M. J. Dorcas, from the Chemistry Department at Harvard; the writer joined the two in the autumn, and work began in earnest on *Valonia* at the Biological Station.

This year was possibly the happiest in Osterhout's life; he had not been out of the United States since his student days in Germany, there were no interruptions, and he enjoyed the calm beauty of Bermuda (without automobiles then). His knee, injured in a mountain climb just before, prevented much walking, but there was the daily row back and forth between the Grasmere Hotel (where we lived) and Agar's Island (where we worked). Dorcas studied the entrance of CO_2 into the sap and later compared the saps of *Valonia macrophysa* with stranded "sea bottles" (then regarded as *V. ventricosa).* He found large differences, the latter cell not accumulating potassium at all. The anomaly was shifted to another genus when the writer identified the Bermuda "sea bottle" as a *Halicystis* (from a different natural order) and named it *H. Osterhoutii.* But the Pacific Coast *Halicystis* does accumulate K! In 1923, Osterhout made the first measurements of potential difference across the protoplasm of *Valonia,* using a Compton electrometer. The P.D. was small (five to ten millivolts), but could be greatly increased by immersing the cell in natural or artificial sap, indicating a pronounced asymmetry of the protoplasm. The cause of such asymmetry (found in several marine algae) is still not thoroughly understood fifty years later. It is formally explained, and in *Halicystis* demonstrated by vacuolar perfusion, that the cell's plasma membrane and its tonoplast differ in their relative permeability to ions.

Osterhout enjoyed the lively scene at the Hamilton waterfront market on Saturday nights; there were tropical fruits, brought in from the West Indies and exposed for sale under kerosene lamps, with haggling over price and condition often becoming intense. Such evenings might end in having a beer at the Windsor Palm Garden, but more often in listening to the Salvation Army songs and preaching. Perhaps these awoke boyhood memories of Baptist services (which left little other trace except a good fund of biblical quotations). At this time he also began taking black and white pictures of sunsets with a simple Brownie camera; some were quite spectacular. It was his only hobby. He was given a folding vest-pocket Kodak for Christmas that year, but he preferred the Brownie. He had a suspicion of complicated apparatus and always did experiments as simply as possible. He literally lived in his work; he kept a pad of paper beside his bed at night, on which he could write, in large flowing script, suggestions for the next day's experiments.

He had to return to Cambridge to offer his course shortly after Christmas; in February Jacques Loeb came to Bermuda on a holiday, only to die of a heart attack within a week. Loeb's death ended the friendship that began in 1892. But it created a vacancy in the Department of General Physiology at the Rockefeller Institute, to which Osterhout was called a year later. He accepted gladly, for although he had been a most successful teacher at Harvard, he had longed for time to do more research. The opportunity now presented, to attack the many problems posed by large algal cells, with adequate staff and fine equipment at the Institute, was irresistible. He gave his last class in the spring of 1925, turned over his three remaining graduate students to his successor, W. J. Crozier, and moved to New York that autumn. With him went E. S. Harris and Marian Irwin, to be joined by the writer in 1926. In Bermuda a branch laboratory was set up in the Grasmere Hotel, with E. B. Damon and W. C. Cooper, Jr., succeeding Dorcas.

Then began the most productive decade of Osterhout's life. The Institute was a scientific paradise, with full time available for research, and many associates, assistants, and technicians to help him. The electrical measurements begun at Harvard on *Nitella* were now pursued intensively by Harris, particularly with regard to the effects of salts on the potential. Osterhout discovered, in collaboration with Harris and the writer, that a "disturbance," a potential variation very like that of a nerve impulse, passed down the cell at a rate of about a centimeter per second, when the cell was stimulated in a variety of ways: electrical, chemical, thermal, etc. While this had been partially appreciated by Georg Hörmann in 1898, it had been unstudied until 1926 when amplifiers and faster recording instruments (Einthoven string galvanometer) allowed it to be followed in detail. (K. Umrath's papers began to appear three years later.) A large number of papers, too numerous to refer to individually, by Osterhout and Harris, later by Osterhout and S. E. Hill, exploited this discovery, and uncovered many interesting analogies to nerve: fatigue, block, alternans rhythm, as well as a most notable difference—conduction through a salt bridge to another cell. The mobilities of a number of ions in the cell surface were investigated, both under normal conditions and with seasonal alterations, effects of nonelectrolytes, and other agents. The bibliography during the decade 1930–1940 indicates the wide range of these studies.

Meanwhile, in Bermuda, Cooper was carrying on studies of the penetration of weak acids and bases, such as H_2S, H_2CO_3, and NH_3, into the vacuole of *Valonia*. It was found that these penetrated more rapidly as undissociated molecules than as charged ions and were therefore under control of the external pH value. Ammonia actually *accumulated* in the vacuole, e.g., up to 0.1 M NH_4Cl from 0.005 M in the seawater. This caused the *Valonia* cells to float and was a tempting analog to the accumulation of potassium. However, the latter was not under very great control by pH.

The laboratory next moved to an old part of "Undercliff," near the Grasmere, where E. B. Damon, A. G. Jacques, and L. L. Burgess worked on bioelectric and chemical properties of the cells. In New York, and later in Bermuda, the writer continued studies of the electrical resistance and capacity of *Valonia, Nitella,* and *Halicystis,* and Marian Irwin studied the penetration of vital dyes in cells and models. The latter two investigators published their results independently, the others usually collaborated with

Osterhout, who became more and more the writer of his assistants' results. Almost every weekend was spent in the country, writing or calculating; the load was heavy and the literary quality of the papers occasionally suffered. In the decade 1926–1936, some fifty joint papers appeared, as well as many by Osterhout alone. It is not surprising that important points were inserted as footnotes, often in proof. The result made for difficult reading, and since no book summing up this work has ever appeared, a great deal of important material is still buried in footnotes, remaining to be rediscovered by future workers.

A totally different research also developed along the line of ingenious models, by which the penetration of electrolytes into cells could be partially explained. Particularly striking was a mixture of *p*-cresol and guaiacol, separating two aqueous phases of different pH. Accumulation of salt occurred on the acid side (= "vacuole"), potassium being preferentially accumulated over sodium. In the research on such systems Osterhout was assisted by S. E. Kamerling, J. W. Murray, and W. M. Stanley (who was later to become a Nobel laureate and famous for "crystallizing" tobacco mosaic virus). Theodore Shedlovsky, Lewis Longsworth, and D. A. MacInnes were especially helpful in the physicochemical analysis of these models. One important concept developed from these studies was that of "carrier molecules," still a useful principle in discussions of cellular permeability.

Although Osterhout had not visited Europe since his student days in Bonn, he was now able to travel again, and attended the Botanical Congress at Cambridge, England, in 1930, saw the Passion Play at Oberammergau, and visited the French Colonial Exposition in Paris. He returned again in 1932 to France and Holland, seeing de Vries once more. He had earlier undergone an operation for glaucoma, saving one eye, but its sight deterioriated slowly henceforth. In the winter of 1933 came an attack of atrial fibrillation, when he was sixty-one. It was brought under control with digitalis and other drugs, but it appeared at the time that his activity must be greatly curtailed. He was actually to live more than thirty years longer, owing to expert medical care and devoted home nursing. He married Marian Irwin at this time. (His first marriage had ended in divorce the year before.)

His department began to break up; Damon and the writer departed to other positions, as did Hill later. Jacques was drowned in Bermuda in 1938, and the Bermuda laboratory was given up. Most of the work of the next two decades was carried on by Mrs. Osterhout and a number of technicians. It is remarkable that so much important research was still accomplished and so many papers written (fifteen in 1935 alone). In 1941 the whole volume of the *J.G.P.* was devoted to articles by friends and associates, in honor of his seventieth birthday. Osterhout never returned to Bermuda, but went regularly to Cold Spring Harbor or Woods Hole in the summers and attended the spring meetings of the National Academy of Sciences until about 1950. As his eyesight failed he kept in touch with developments by having others read to him, and he dictated papers after he could no longer see. Curiously, several of his later papers were on the egg of *Nereis,* a marine worm, his only work with animals. His last paper was a "summing up," written for the *Annual Review of Plant Physiology;* readers are referred to it for further details of his work.

In his last few years he was bedridden, but he retained clarity of intellect and dignity of bearing to the last. Winthrop Osterhout died peacefully in St. Barnabas Hospital in New York on April 9, 1964. His ashes are buried in the churchyard of St. James the Less in Philadelphia, along with those of Marian Irwin Osterhout, who died in 1973.

CHRONOLOGY

1871	Born Brooklyn, N.Y., August 2
1889	Graduated from Providence (R.I.) High School; entered Brown University
1892	Attended the Botany Course at the Marine Biological Laboratory, Woods Hole, Massachusetts
1893	A.B., Brown University
1893–1895	Instructor in Botany, Brown University
1894	M.A., Brown University
1894–1895	Instructor in Botany (summers), Marine Biological Laboratory, Woods Hole
1895–1896	Student of Eduard Strasburger, Bonn University
1896	First paper published, in *Annals of Botany*
1896–1901	Instructor in Botany, University of California
1899	Ph.D., University of California
	Married Anna Maria Landstrom, Berkeley, California
1901	Assistant Professor of Botany, University of California
1905	*Experiments with Plants* published
1907	Associate Professor, University of California
1909	Assistant Professor of Botany, Harvard University
1910	*Agriculture for Schools of the Pacific Slope* published (with E. W. Hilgard)
	Fellow, American Academy of Arts and Sciences
1913	Professor of Botany, Harvard University
1917	Member, American Philosophical Society
1918	*Journal of General Physiology* founded (with Jacques Loeb)
1919	Elected to National Academy of Sciences
	Trustee, Marine Biological Laboratory
	Hitchcock Lecturer, University of California
1920	Member, Board of Scientific Directors, Rockefeller Institute for Medical Research
1922	Colver Lecturer, Brown University
	Lowell Lecturer (Boston)
1923	Began work on *Valonia,* Bermuda Biological Station
1925	Sedgwick Lecturer, Massachusetts Institute of Technology
	D.Sc. (Hon.), Harvard University
	Member of the Rockefeller Institute

1926	D.Sc. (Hon.), Brown University
1929	Attended International Physiological Congress (Boston)
1930	Attended International Botanical Congress (Cambridge, England)
1933	Married (2d) Marian Irwin, New Castle, Delaware
1939	Member Emeritus, Rockefeller Institute
1957	Last paper published *(Annual Review of Plant Physiology)*
1964	Died, New York City, April 9

MEMBERSHIPS

Member, National Academy of Sciences

Corresponding Member, Botanical Society of Edinburgh; Kungliga Fysiografiska Sällskapet, Lund; Kaiserlich Leopold-Carolinische deutsche Akademie der Naturforscher (Halle); Academy of Natural Sciences (Philadelphia)

Member, Washington and New York Academies of Science, American Society of Plant Physiologists, Botanical Society of America, Society of General Physiologists, American Society of Naturalists, American Philosophical Society, American Chemical Society, American Physiological Society, Society for Experimental Biology and Medicine

Fellow, American Academy of Arts and Sciences, American Association for the Advancement of Science

BIBLIOGRAPHY

This bibliography was greatly aided by one assembled by Nina Kobelt, Osterhout's secretary at the Rockefeller Institute.

KEY TO ABBREVIATIONS

Am. J. Botany = American Journal of Botany
Biol. Bull. = Biological Bulletin
Bot. Gaz. = Botanical Gazette
Bot. Rev. = Botanical Review
Cold Spring Harbor Symp. Quant. Biol. = Cold Spring Harbor Symposia on Quantitative Biology
Jahrb. wissensch. Bot. = Jahrbücher für wissenschaftliche Botanik
J. Biol. Chem. = Journal of Biological Chemistry
J.G.P. = Journal of General Physiology
Proc. Nat. Acad. Sci. = Proceedings of the National Academy of Sciences
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society for Experimental Biology and Medicine
Univ. Calif. Publ. Bot. = University of California Publications in Botany

1896

On the life-history of *Rhabdonia tenera,* J. Ag. Annals of Botany, 10:403–27. 2 plates.

With W. A. Setchell. Some aqueous media for preserving algae for class material. Bot. Gaz., 21:140–41.

A simple freezing device. Bot. Gaz., 21:195.

1897

Über Entstehung der karyokinetischen Spindel bei *Equisetum.* Jahrb. wissensch. Bot., 30:159–65.

1898

Problems of heredity. University Chronicle (Berkeley), 1:311–15.

1900

Befruchtung bei *Batrachospermum.* Flora, 87:109–15.

1902

Cell studies. I. Spindle formation in *Agave.* Proceedings of the California Academy of Sciences, 2:255–65.

1904

Contributions to cytological technique. Univ. Calif. Publ. Bot., 2:73–75.

1905

Experiments with Plants. New York, The Macmillan Company. xix + 492 pp. (With many reprintings and at least two translations, one into Dutch, 1909, and one by N. A. Maximov in Russian, in the late 1920s.)

1906

The resistance of certain marine algae to changes in osmotic pressure and temperature. Univ. Calif. Publ. Bot., 2:227–28.

The role of osmotic pressure in marine plants. Univ. Calif. Publ. Bot., 2:229–30.

On the importance of physiologically balanced solutions for plants. Univ. Calif. Publ. Bot., 2:231–34.

The antitoxic action of potassium on magnesium. Univ. Calif. Publ. Bot., 2:235–36.

Extreme toxicity of sodium chloride and its prevention by other salts. J. Biol. Chem., 1:363–69.

On the importance of physiologically balanced solutions for plants. I. Marine plants. Bot. Gaz., 42:127–34.

1907

On the importance of physiologically balanced solutions for plants. II. Fresh-water and terrestrial plants. Bot. Gaz., 44:259–72.

On nutrient and balanced solutions. Univ. Calif. Publ. Bot., 2: 317–18.

1908

The antagonistic action of magnesium and potassium. Bot. Gaz., 45:117–24.

The value of sodium to plants by reason of its protective action. Univ. Calif. Publ. Bot., 3:331–37.

On the effects of certain poisonous gases on plants. Univ. Calif. Publ. Bot., 3:339–40.

On plasmolysis. Bot. Gaz., 46:53–55.

Weitere Untersuchungen über die Ubereinstimmung der Salzwirkungen bei Tieren und Pflanzen. Die Schützwirkung des Natriums für Pflanzen. Jahrb. wissensch. Bot., 46:121–36.

1909

Proeven met planten. Translated by S. J. Geerts-Ronner. The Netherlands.

The nature of balanced solutions. Bot. Gaz., 47:48–49.

On similarity in the behavior of sodium and potassium. Bot. Gaz., 48:98–104.

1910

With E. W. Hilgard. *Agriculture for Schools of the Pacific Slope.* New York, The Macmillan Company. xix + 428 pp.

On the penetration of inorganic salts into living protoplasm. Zeitschrift für physikalische Chemie, 70:408–13.

1911

The permeability of living cells to salts in pure and balanced solutions. Science, 34:187–89.

1912

The permeability of protoplasm to ions and the theory of antagonism. Science, 35:112–15.

Plants which require sodium. Bot. Gaz., 54:532–36.

Reversible changes in permeability produced by electrolytes. Science, 36:350–52.

Some chemical relations of plants and soil. Science, 36:571–76.

1913

The effect of anesthetics upon permeability. Science, 37:111–12. Also in Proceedings of the American Physiological Society (1911–12), 29:xi.

The organization of the cell with respect to permeability. Science, 38:408–9.

Protoplasmic contractions resembling plasmolysis which are caused by pure distilled water. Bot. Gaz., 55:446–51.

Some quantitative researches on the permeability of plant cells. Plant World, 16:129–44.

1914

The chemical dynamics of living protoplasm. Science, 39:544–46.

The effect of alkali on permeability. J. Biol. Chem., 19:335–43.

The effect of acid on permeability. J. Biol. Chem., 19:493–501.

Antagonism between acids and salts. J. Biol. Chem., 19:517–20.

Quantitative criteria of antagonism. Bot. Gaz., 58:178–86.

The measurement of antagonism. Bot. Gaz., 58:272–76.

The forms of antagonism curves as affected by concentration. Bot. Gaz., 58:367–71.

Stetige Änderungen in den Formen von Antagonismus-Kurven. Jahrb. wissensch. Bot., 54:645–50.

Über den Temperaturkoeffizienten des elektrischen Leitvermögens im lebenden und toten Gewebe. Biochemische Zeitschrift, 67: 272–77.

Vitality and injury as quantitative conceptions. Science, 40:488–91.

1915

Extreme alterations of permeability without injury. Bot. Gaz., 59:242–53.

On the decrease of permeability due to certain bivalent kations. Bot. Gaz., 59:317–30.

The effects of some trivalent and tetravalent kations on permeability. Bot. Gaz., 59:464–73.

The determination of additive effects. Bot. Gaz., 60:228–34.

The measurement of toxicity. J. Biol. Chem., 23:67–70.

Normal and abnormal permeability. Am. J. Botany, 2:93–94.

On the nature of antagonism. Science, 41:255–56.

1916

The decrease of permeability produced by anesthetics. Bot. Gaz., 61:148–58.

A dynamical theory of antagonism. Proceedings of the American Philosophical Society, 55:533–53.

The dynamics of antagonism. Science, 43:721.

Eduard Strasburger (1844–1912). Proceedings of the American Academy of Arts and Sciences, Vol. 51, No. 14.

The nature of mechanical stimulation. Proc. Nat. Acad. Sci., 2:237–39.

Permeability and viscosity. Science, 43:857–59.

Antagonism and Weber's Law. Science, 44:318–20.

The penetration of balanced solutions and the theory of antagonism. Science, 44:395–96.

Specific action of barium. Am. J. Botany, 3:481–82.

1917

Antagonism and permeability. Science, 45:97–103.

The dynamics of the process of death. J. Biol. Chem., 31:585–89. Also in Science, 46:542.

Some aspects of the temperature coefficients of life processes. J. Biol. Chem., 32:23–27.

With A. R. C. Haas. An adaptation of Winkler's method to biological work. J. Biol. Chem., 32:141–46.

With A. R. C. Haas. The dynamics of photosynthesis. Science, 46:343.

The role of the nucleus in oxidation. Science, 46:367–69.

Similarity in the effects of potassium cyanide and of ether. Bot. Gaz., 63:77–80.

Tolerance of fresh water by marine plants and its relation to adaptation. Bot. Gaz., 63:146–49.

Does the temperature coefficient of permeability indicate that it is chemical in nature? Bot. Gaz., 63:317–20.

1918

The basis of measurement of antagonism. J. Biol. Chem., 34:363–68.

The determination of buffer effects in measuring respiration. J. Biol. Chem., 35:237–40.

Conductivity as a measurement of permeability. J. Biol. Chem., 36:485–88.

A demonstration of photosynthesis. Am. J. Botany, 5:105–11.

With A. R. C. Haas. Dynamical aspects of photosynthesis. Proc. Nat. Acad. Sci., 4:85–91.

Endurance of extreme conditions and its relation to the theory of adaptation. Am. J. Botany, 5:507–10.

With A. R. C. Haas. On the dynamics of photosynthesis. J.G.P., 1:1–16.

A method of studying respiration. J.G.P., 1:17–22.

An indicator method of measuring the consumption of oxygen. J.G.P., 1:167–69.

Note on the effect of diffusion upon the conductivity of living tissues. J. Biol. Chem., 36:489–90.

A method of measuring the electrical conductivity of living tissues. J. Biol. Chem., 36:557–68.

With A. R. C. Haas. A simple method of measuring photosynthesis. Science, 47:420–22.

Note on measuring the relative rates of life processes. Science, 48:172–74.

The nucleus as a center of oxidation. Brooklyn Botanical Garden Memoirs, 1:342–47.

A simple method of demonstrating the production of aldehyde by chlorophyll and by aniline dyes in the presence of sunlight. Am. J. Botany, 5:511–13.

Comparative studies of respiration. I. Introduction. J.G.P., 1: 171–79.

1919

With A. R. C. Haas. The temperature coefficient of photosynthesis. J.G.P., 1:295–98.

A comparative study of permeability in plants. J.G.P., 1:299–304.

Decrease of permeability and antagonistic effects caused by bile salts. J.G.P., 1:405–8.

A comparison of permeability in plant and animal cells. J.G.P., 1:409–13.

Antagonism between alkaloids and salts in relation to permeability. J.G.P., 1:515–19.

Comparative studies on respiration. VII. Respiration and antagonism. Introductory note. J.G.P., 2:1–4.

Apparatus for the study of photosynthesis and respiration. Bot. Gaz., 68:60–62.

1920

The mechanism of injury and recovery. J.G.P., 3:15–20.

A theory of injury and recovery. I. Experiments with pure salts. J.G.P., 3:145–56.

1921

A theory of injury and recovery. II. Experiments with mixtures. J.G.P., 3:415–29.

A theory of injury and recovery. III. Repeated exposures to toxic solutions. J.G.P., 3:611–22.

Conductivity and permeability. J.G.P., 4:1–9.

The mechanism of injury and recovery of the cell. Science, 53:352–56.

1922

Direct and indirect determinations of permeability. J.G.P., 4:275–83.

Injury, recovery and death. American Journal of Physiology, 59: 443.

Some aspects of selective absorption. J.G.P., 5:225–30.

1923

Exosmosis in relation to injury and permeability. J.G.P., 5:709–25.

Injury, Recovery and Death in Relation to Conductivity and Permeability. Monograph on experimental biology. Philadelphia, J. B. Lippincott Company. 259 pp. (Reviewed in J. Am. Chem. Soc., 45:1861.)

The mechanism of injury, recovery and death. Harvey Lectures, 17:174–200.

Continuation of investigations on permeability in cells. Carnegie Institution of Washington Year Book, 22:290.

The Nature of Life. New York, Henry Holt & Co. 117 pp. (Colver Lectures, Brown University, 1922.)

1924

Jacques Loeb, the scientist. Proc. Soc. Exp. Biol. Med., 21:iv; also in Science, 59:428.

1925

On the importance of maintaining certain differences between cell sap and external medium. J.G.P., 7:561–64.

With M. J. Dorcas. Contrasts in the cell sap of *Valonia* and the problem of flotation. J.G.P., 7:633–40.

Is living protoplasm permeable to ions? J.G.P., 8:131–46.

With M. J. Dorcas. The penetration of CO_2 into living protoplasm. J.G.P., 9:255–67.

1926

The behavior of electrolytes in *Valonia.* Proc. Soc. Exp. Biol. Med., 24:234–35.

1927

Some aspects of bioelectrical phenomena. J.G.P., 11:83–99.

With E. B. Damon and A. G. Jacques. Dissimilarity of inner and outer protoplasmic surfaces in *Valonia.* J.G.P., 11:193–205.

Some Fundamental Problems of Cellular Physiology. (3d William Thompson Sedgwick Memorial Lecture) New Haven, Yale University Press. 55 pp.

1928

Jacques Loeb. J.G.P., 8:ix–lix.

Jacques Loeb. Collecting Net, 25:7.

With E. S. Harris. Protoplasmic asymmetry in *Nitella* as shown by bioelectric measurements. J.G.P., 11:391–406.

With E. S. Harris. The death wave in *Nitella.* I. Application of like solutions. J.G.P., 12:167–86.

With A. G. Jacques. Internal vs. external toxicity in *Valonia.* J.G.P., 12:209–19.

With E. S. Harris. Reversible changes in living protoplasm. Proc. Soc. Exp. Biol. Med., 26:124–25.

Note on the penetration of electrolytes. Proc. Soc. Exp. Biol. Med., 26:192–97.

Some aspects of cellular physiology. In: *Lectures on Plant Pathology and Physiology in Relation to Man,* pp. 179–90 (Mayo Foundation Lectures, 1926–27). Philadelphia, W. B. Saunders Company.

1929

With E. S. Harris. The death wave in *Nitella.* II. Applications of unlike solutions. J.G.P., 12:355–61.

With W. C. Cooper, Jr., and M. J. Dorcas. The penetration of strong electrolytes. J.G.P., 12:427–33.

With E. S. Harris. The concentration effect in *Nitella.* J.G.P., 12:761–81.

With E. S. Harris. Note on the nature of the current of injury in tissues. J.G.P., 13:47–56.

With L. R. Blinks and E. S. Harris. Studies on stimulation in *Nitella.* Proc. Soc. Exp. Biol. Med., 26:836–38.

With E. S. Harris. Bioelectrical aspects of the all-or-none law. Proc. Soc. Exp. Biol. Med., 26:838–40.

Some aspects of permeability and bioelectrical phenomena. In: Molecular physics in relation to biology. Bulletin of the National Research Council, 69:170–228.

1930

With E. B. Damon. The concentration effect with *Valonia:* potential differences with concentrated and diluted sea water. J.G.P., 13:445–57.

With S. E. Hill. Negative variations in *Nitella* produced by chloroform and by potassium chloride. J.G.P., 13:459–67.

With S. E. Hill. Salt bridges and negative variations. J.G.P., 13:547–52.

With A. G. Jacques. The kinetics of penetration. II. The penetration of CO_2 into *Valonia.* J.G.P., 13:695–713.

Calculations of bioelectrical potentials. I. Effects of KCl and NaCl on *Nitella.* J.G.P., 13:715–32.

With W. C. Cooper, Jr. The accumulation of electrolytes. I. The entrance of ammonia into *Valonia macrophysa.* J.G.P., 14:117–25.

The kinetics of penetration. III. Equations for the exchange of ions. J.G.P., 14:277–84.

The accumulation of electrolytes. II. Suggestions as to the nature of accumulation in *Valonia.* J.G.P., 14:285–300.

With A. G. Jacques. The accumulation of electrolytes. III. Behavior of sodium, potassium and ammonium in *Valonia.* J.G.P., 14:301–14.

1931

Electrical phenomena in the living cell. Harvey Lectures, 25:169–85, 1929–30.

With S. E. Hill. The death wave in *Nitella.* III. Transmission. J.G.P., 14:385–92.

With S. E. Hill. Electrical variations due to mechanical transmission of stimuli. J.G.P., 14:473–85.

With S. E. Hill. The production and inhibition of action currents by alcohol. J.G.P., 14:611–16.

Physiological studies of single plant cells. Biological Reviews, 6: 369–411.

1932

With A. G. Jacques. The accumulation of electrolytes. IV. Internal versus external concentrations of potassium. J.G.P., 15:537–50.

With W. M. Stanley. The accumulation of electrolytes. V. Models showing accumulation and a steady state. J.G.P., 15:667–89.

The kinetics of penetration. IV. Diffusion against a growing potential gradient in models. J.G.P., 16:157–63.

With W. M. Stanley. Models showing accumulation. Proc. Soc. Exp. Biol. Med., 29:577–78.

Studies on large plant cells. Australian Journal of Experimental Biology and Medical Science, 9:135–39.

1933

The kinetics of penetration. V. The kinetics of a model as related to the steady state. J.G.P., 16:529–57.

With S. E. Hill. Anesthesia produced by distilled water. J.G.P., 17:87–98.

Anesthesia in acid and alkaline solutions. J.G.P., 17:99–103.

The electrical behavior of large plant cells. Cold Spring Harbor Symp. Quant. Biol., 1:125–30. Also in Collecting Net, 8:213–14.

Osmotic pressure in relation to permeability in large plant cells and in models. Cold Spring Harbor Symp. Quant. Biol., 1:166–69.

Permeability in large plant cells and in models. Ergebnisse der Physiologie, 35:967–1021.

Some aspects of cell physiology. Annals of Internal Medicine, 7:396–400.

With S. E. Hill. Reversible loss of the potassium effect in distilled water. J.G.P., 17:105–8.

1934

With S. E. Kamerling and W. M. Stanley. The kinetics of penetration. VI. Some factors affecting penetration. J.G.P., 17:445–67.

With S. E. Kamerling and W. M. Stanley. The kinetics of penetration. VII. Molecular vs. ionic transport. J.G.P., 17:469–80.

With S. E. Kamerling. The kinetics of penetration. VIII. Temporary accumulation. J.G.P., 17:507–16.

With A. G. Jacques. The accumulation of electrolytes. VI. The effect of external pH. J.G.P., 17:727–50.

Nature of the action currents in *Nitella.* I. General considerations. J.G.P., 18:215–27.

With S. E. Kamerling. The kinetics of penetration. IX. Models of mature cells. J.G.P., 18:229–34.

With A. G. Jacques. Penetration of potassium into *Nitella.* Proc. Soc. Exp. Biol. Med., 31:1121–22.

1935

With S. E. Hill. Positive variations in *Nitella.* J.G.P., 18:369–75.

With S. E. Hill. Nature of the action current in *Nitella.* II. Special cases. J.G.P., 18:377–83.

With S. E. Hill. Nature of the action current in *Nitella.* Some additional features. J.G.P., 18:499–514.

With S. E. Hill. Restoration of the potassium effect by means of action currents. J.G.P., 18:681–86.

With S. E. Hill. Mechanical restoration of irritability and of the potassium effect. J.G.P., 18:687–94.

With A. G. Jacques. The kinetics of penetration. XI. Entrance of potassium into *Nitella.* J.G.P., 18:967–85.

Chemical restoration in *Nitella.* I. Ammonia and some of its compounds. J.G.P., 18:987–95.

With S. E. Kamerling. The accumulation of electrolytes. VIII. The accumulation of KCl in models. J.G.P., 19:167–78.

With S. E. Hill. Pacemakers in *Nitella.* I. Temporary local differences in rhythm. J.G.P., 19:307–9.

How do electrolytes enter the cell? Proc. Nat. Acad. Sci., 21:125–32.

How do electrolytes penetrate the cell? Collecting Net, 10:1–8.

With S. E. Hill. The role of ions in *Valonia* and *Nitella.* Biol. Bull., 69:329.

Some experimental modifications of the protoplasmic surface. Proc. Soc. Exp. Biol. Med., 32:715–16.

With S. E. Hill. Some aspects of anesthesia and irritability. Science, 81:418–19.

Mechanism of salt absorption by plant cells. Nature, 136:1034–35.

1936

Chemical restoration in *Nitella.* II. Restorative action of blood. J.G.P., 19:423–25.

Electrical phenomena in large plant cells. Physiological Reviews, 16:216–37.

The absorption of electrolytes in large plant cells. Bot. Rev., 2:283–315.

Über einige chemische und elektrische Eigenschaften von protoplasmaoberflächen. Kolloid-Zeitschrift, 77:373–85.

With S. E. Hill. Some ways to control bioelectrical behavior. Cold Spring Harbor Symp. Quant. Biol., 4:43–52.

Changes of apparent ionic mobilities in protoplasm. I. Effects of guaiacol on *Valonia.* J.G.P., 20:13–43.

1937

Changes of apparent ionic mobilities in protoplasm. II. The action of guaiacol as affected by pH. J.G.P., 20:685–93.

Electrochemical methods in the study of plant cells. Transactions of the Electrochemical Society, 71:93–99.

The protoplasmic surface in certain plant cells. Transactions of the Faraday Society, 33:997–1002.

1938

With S. E. Hill. Calculations of bioelectric potentials. II. The concentration potential of KCl in *Nitella.* J.G.P., 21:541–56.

Effects of potassium on the potential of *Halicystis.* J.G.P., 21:631–34.

With A. G. Jacques. The accumulation of electrolytes. X. Accumulation of iodine by *Halicystis* and *Valonia.* J.G.P., 21:687–93.

Changes of apparent ionic mobilities in protoplasm. III. Some effects of guaiacol on *Halicystis.* J.G.P., 21:707–20.

With A. G. Jacques. The accumulation of electrolytes. XI. Accumulation of nitrate by *Valonia* and *Halicystis.* J.G.P., 21:767–73.

With S. E. Hill. Nature of the action current in *Nitella.* IV. Production of quick action currents by exposure to NaCl. J.G.P., 22:91–106.

With S. E. Hill. Delayed potassium effect in *Nitella.* J.G.P., 22:107–13.

With S. E. Hill. Pacemakers in *Nitella.* II. Arrhythmia and block. J.G.P., 22:115–30.

With S. E. Hill. Calculations of bioelectric potentials. IV. Some effects of calcium on potentials in *Nitella.* J.G.P., 22:139–46.

With J. W. Murray. The movement of water from concentrated to dilute solutions through liquid membranes. Science, 87:430. (A)

With J. W. Murray. Movement of water against a gradient in models. Proc. Soc. Exp. Biol. Med., 38:468–70.

Potentials in *Halicystis* as affected by non-electrolytes. Proc. Nat. Acad. Sci., 24:75–76.

With S. E. Hill. Calculations of bioelectric potentials. III. Variation in partition coefficients and ion mobilities. Proc. Nat. Acad. Sci., 24:312–15.

With S. E. Hill. Reversal of the potassium effect in *Nitella.* Proc. Nat. Acad. Sci., 24:427–29.

1939

Changes of apparent ionic mobilities in protoplasm. IV. Influence of guaiacol on the effects of sodium and potassium in *Nitella.* J.G.P., 22:417–27.

Calculations of bioelectric potentials. V. Potentials in *Halicystis.* J.G.P., 23:53–57.

Calculations of bioelectric potentials. VI. Some effects of guaiacol on *Nitella.* J.G.P., 23:171–76.

With S. E. Hill. Chemical restoration in *Nitella.* III. Effects of inorganic salts. Proc. Nat. Acad. Sci., 25:3–5.

With J. W. Murray. Note on water in non-aqueous solutions. Science, 90:397–98.

1940

Alfred George Jacques. Science, 91:133–34.

With J. W. Murray. Behavior of water in certain heterogeneous systems. J.G.P., 23:365–90.

Some chemical aspects of the potassium effect. J.G.P., 23:429–32.

Effects of hexylresorcinol on *Nitella.* J.G.P., 23:569–73.

With S. E. Hill. Action curves with single peaks in *Nitella* in relation to the movement of potassium. J.G.P., 23:743–48.

Effects of guaiacol and hexylresorcinol in the presence of barium and calcium. J.G.P., 23:749–51.

Chemical restoration in *Nitella.* IV. Effects of guanidine. J.G.P., 24:7–8.

With S. E. Hill. The experimental production of double peaks in *Chara* action curves and their relation to the movement of potassium. J.G.P., 24:9–13.

Some models of protoplasmic surfaces. Cold Spring Harbor Symp. Quant. Biol., 8:51–52.

1941

Effects of hexylresorcinol on *Valonia.* J.G.P., 24:311–13.

Effects of nitrobenzene and benzene on *Valonia.* J.G.P., 24:699–702.

Positive potentials due to aniline and the antagonistic action of ammonia. Journal of Cellular and Comparative Physiology, 18:129–35.

1942

Increased irritability in *Nitella* due to guanidine. J.G.P., 26:65–73.

1943

Diffusion potentials in models and in living cells. J.G.P., 26:293–307.

Pacemakers in *Nitella*. III. Electrical alternans. J.G.P., 26:457–65.

Nature of the action current in *Nitella*. V. Partial response and the all-or-none law. J.G.P., 27:61–68.

A model of the potassium effect. J.G.P., 27:91–100.

Studies of the inner and outer surfaces of large plant cells. I. Plasmolysis due to salts. J.G.P., 27:139–42.

William Albert Setchell (1864–1943). American Philosophical Society Yearbook, pp. 431–32.

1944

Studies of the inner and outer protoplasmic surfaces of large plant cells. J.G.P., 28:17–22.

Differing rates of death at inner and outer surfaces of the protoplasm. I. Effects of formaldehyde on *Nitella*. J.G.P., 28:23–36.

Differing rates of death at inner and outer surfaces of the protoplasm. II. Negative potential in *Nitella* caused by formaldehyde. J.G.P., 28:37–41.

Differing rates of death at inner and outer surfaces of the protoplasm. III. Effects of mercuric chloride on *Nitella*. J.G.P., 28:343–47.

1945

Effects of hydroxyl on negative and positive cells of *Nitella*. J.G.P., 29:43–56.

Water relations in the cell. I. The chloroplasts of *Nitella* and of *Spirogyra*. J.G.P., 29:73–78.

1946

Some properties of protoplasmic gels. I. Tension in the chloroplast of *Spirogyra*. J.G.P., 29:181–92.

Nature of the action current in *Nitella*. VI. Simple and complex action patterns. J. G. P., 30:47–59.

1947

Some properties of protoplasmic gels. II. Contraction of chloroplasts in currents of water entering the cell and expansion in outgoing currents. J.G.P., 30:229–34.

The absorption of electrolytes in large plant cells. II. Bot. Rev., 13:194–215.

Some aspects of secretion. I. Secretion of water. J.G.P., 30:439–47.

1948

Abnormal protoplasmic patterns and death in slightly hypertonic solutions. J.G.P., 31:291–300.

Effects of hypertonic solutions on *Nereis* eggs. Biol. Bull., 95:269. (A)

Solubility of the vitelline membrane of *Nereis* eggs. Biol. Bull., 95:269. (A)

Experiments on chloroplasts and on photosynthesis. Biol. Bull., 95:270. (A)

1949

Movements of water in cells of *Nitella*. J.G.P., 32:553–58.

Transport of water from concentrated to dilute solutions in cells of *Nitella*. J.G.P., 32:559–66.

Some bioelectric problems. Proc. Nat. Acad. Sci., 35:548–58.

Extrusion of jelly by eggs of *Nereis limbata* under electrical stimulus. Biol. Bull., 97:260. (A)

1950

Higher permeability for water than for ethyl alcohol in *Nitella*. J.G.P., 33:275–84.

Effects of electrical currents on the absorption of water by eggs of *Nereis limbata*. J.G.P., 33:379–88.

Distant effects of toxic agents. J.G.P., 34:279–84.

The mechanism of accumulation. Biol. Bull., 99:308. (A)

Activation of *Nereis* eggs by a detergent. Biol. Bull., 99:362. (A)

Relative solubility of the components of the *Nereis* egg. Biol. Bull., 99:362. (A)

1951

Injury in relation to cell organization. J.G.P., 34:321–23.

Behavior of jelly in eggs of *Nereis limbata*. Biol. Bull., 101:226. (A)

Detergent action of sperm extract in *Nereis limbata*. Biol. Bull., 101:226. (A)

1952

Some aspects of protoplasmic motion. J.G.P., 35:519–27.

Mechanism of accumulation in living cells. J.G.P., 35:579–94.

Activation of eggs of *Nereis limbata* by a surface active extract of dead sperm. Biol. Bull., 103:305–6. (A)

Reversible contraction of protoplasmic structures by changes in pH values. Biol. Bull., 103:306. (A)

1953

Protamin in an extract of the sperm of *Nereis limbata*. Biol. Bull., 105:379–80. (A)

Surface active material obtained from *Nereis limbata*. Biol. Bull., 105:380. (A)

With Theodore Shedlovsky. Surface active properties of an extract of the sperm of *Nereis limbata*. Biol. Bull., 105:383–84. (A)

1954

Changes in resting potential due to a shift of electrolytes in the cell produced by non-electrolytes. J.G.P., 37:423–32.

Apparent violations of the all-or-none law in relation to potassium in the protoplasm. J.G.P., 37:813–24.

Note on the work of Jacques Loeb. In: *Ion Transport Across Membranes,* pp. 1–2. New York, Academic Press, Inc.

Reversible clotting in *Spirogyra*. Biol. Bull., 107:317. (A)

1955

Reversible shrinkage in *Chaetomorpha*. Biol. Bull., 109:366. (A)

Apparent violations of the all-or-none law in relation to potassium in the protoplasm. In: *Electrochemistry in Biology and Medicine,* ed. by T. Shedlovsky, pp. 213–24. New York, John Wiley & Sons, Inc.

1956

The role of water in protoplasmic permeability and in antagonism. J.G.P., 39:963–76.

Effect of electric current on the contraction of the chloroplasts of *Spirogyra*. Biol. Bull., 111:310. (A)

1957

The use of aquatic plants in the study of some fundamental problems. Annual Review of Plant Physiology, 8:1–10.