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LAWRENCE ROGERS BLINKS
1900—1989

A Biographical Memoir by

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Photograph Courtesy Hopkins Marine Station.

Lawrence R Blinks

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BY ISABELLA A. ABBOTT AND CELIA M. SMITH

FROM THE BEGINNING, LAWRENCE BLINKS'S WORK foreshadowed several of his remarkable contributions that would span his diverse career as a leading electrophysiologist and a pioneering photosynthesis researcher: Nearly all of his efforts were conducted as comparative studies with simple, elegant marine algae, model systems used to generate fundamental contributions with state-of-the-art technologies. The use of electrodes, designed and built by Blinks, unified his research from the Rockefeller Institute to Stanford University's Hopkins Marine Station, from a new Ph.D. in 1926 to retirement, as an avid, lifelong researcher until his death in 1989. His explorations enriched the electrophysiology research of his mentor, the great Osterhout; established the first method, the oxygen electrode, for measuring photosynthesis in rapid timescales; and set the pace for the 1960s "physiological era" of marine ecology (Roughgarden, 1998), the formative years of our nation's marine ecosystem research.

PERSONAL REFLECTIONS ON L. R. BLINKS AT HOPKINS MARINE STATION

The first time that Lawrence Blinks's name came into my life as a person, not as a famous physiologist, was when my husband, Donald P. Abbott, and I were graduate students at the University of California, Berkeley. It was about 1953, Don had been at Hopkins Marine Station at Pacific Grove, California, for two summers assisting in Berkeley's Invertebrate Zoology course that was taught there. After the summer course was over and he had returned to Berkeley, he wrote Blinks, then director of the marine station, to ask permission to come to the station for a weekend of collecting during low tides. In answer he received a key to Agassiz Laboratory in the mail. We laughed at the informality and ease with which permission was granted; at Berkeley in that period it never would have been that easy.

Berkeley faculty always wore suits and ties whether teaching or not, yet when I met Blinks later we found that if he had a tie on, he was going to do one of three things: (1) go to Palo Alto for a faculty meeting; (2) go to see his dentist; or (3) go to see his attorney. Otherwise he was tieless. This practicality and informality turned out to be one of the strongest and most endearing features of this shy person, who in the opinion of the first author allowed the station to attract scholars and budding biologists to study its world-renowned fauna and flora when funds were short for higher education. It was Blinks who brought National Science Foundation (NSF) funds for college-level teachers to come to learn about invertebrates and seaweeds, microbiology, and physiology (both plant and animal) so that those who had been drafted into the armed services in World War II could find intellectual refreshment, and others who had never previously found wonder and joy in working with living creatures could translate their happiness to their students when they got home. Many inspired their students to come to Hopkins to study later; I remember three generations who came.

A somewhat similar but more far-reaching educational experience came in the late 1960s when Stanford initiated its famous undergraduate Spring Course, in which Lawrence

Blinks joined Don Abbott and over the years other Hopkins faculty to offer mainly Stanford undergraduates what was later said to be "a life-determining educational experience." Undergraduates registered for 15 credits on the Monterey Peninsula. For many of them it was the first time away from home or dormitories and their first time to be fully dependent on themselves for housing, housekeeping, laundry, and food shopping and preparation as well as carrying on a bruising field and laboratory research program. It took a while to get over the shock that their research problems might take different times since the ocean and tide pools were run by the tides, not by switching on a light in a laboratory. Disbelief! This guy must be joking! We are to make observations over 24 hours? Almost unanimously students loved this research experience, and people at the station have smiled to hear the stories over and over through the years when these students, now grown up and with children the ages they were when they were in that class, tell stories in which they joyously relive those special springs. Lawrence Blinks said many times that it was the most exhilarating teaching he ever took part in. For eight years I taught in that course, too, and since then I have carried the way of examining different methods of doing research, of testing and evaluating and completely understanding (as the students did) what replication means. (It means getting up at 3 a.m., donning snorkel or scuba gear and going out in the dark to the study site to see what those little snails are doing now: crawling around? or sleeping? or eating? Where are they, if not at "home"? Near the end of the course, when their research was over and written up (after endless versions) and it was time to give oral presentations, the students, who had been given many opportunities to get up to tell in clear, scientific language what they were doing, were often made nervous by two (sometimes more) members of the National Academy of Sciences present to hear their reports. C. B. Van Niel, that master of clarity of thought, was heard to say that some of the presentations were better than the ones he might have heard in Washington, D.C.

Lawrence was director of Hopkins Marine Station from 1943 until 1965, during which time the laboratory began to enlarge its facilities from essentially the Jacques Loeb Laboratory, a Spanish-looking building that dominated Mussel Point and the Agassiz building on the east side of the point, hidden mostly by old cypress trees and tall bushes that were seaside and drought tolerant. In 1950 when my husband and I arrived in Pacific Grove, Loeb lab held a one-room station office and a stock room, with Professor Van Niel's laboratory in one wing on the first floor, and a library upstairs that had the best ocean view from the station. Upstairs one could also find Blinks's office, but the most fascinating room for anyone interested in marine algae was the "room of black magic" downstairs (across from the entrance), where Blinks had a lot of electrical equipment pieced together to measure electric potentials of large-celled green algae (*Nitella, Halicystis,* and *Valonia* species). The room had to be darkened, but that did not prevent my going to visit him as a diversion on the way to or from the library—or even both, as he often remembered something to add to the conversation we just had, and would look for me to finish it. Years later after Blinks had retired, he was moved to the Agassiz building, where I had an office on the top floor with a splendid view of Monterey Bay and Cannery Row. He moved in two doors down the hall from me, with his electrical equipment. I couldn't believe my good luck to have him so close by. We could see and talk to each other for a few minutes every day. And we did. While he was so excellent at making all kinds of mysterious (to me) equipment work, he also shared with me a love for classical music. On hearing about "fast forward" for 8-inch tape decks, he was heard to say that fast forward was just what he needed to hear all the classical music he wanted to hear before he died.

Perhaps because of his gentleness and shyness, he served Stanford well as director of the station in the period, following the Depression and World War II, in which higher education throughout the country, including Stanford University, was forced to survive one financial crisis after another. His biggest contribution to Stanford was to keep the station open while at the same time offering (literally) priceless marine biological experiences. We had extraordinary plants and animals around us from which we could learn so much, and superb teachers to share the information. Beginning before he died in 1989 and continuing since, the station has changed from relying on those wonderful marine plants and animals to be our star attractions, to individual laboratories working on functional and molecular problems that require more than the excellent observation and interpretation of the natural history school. The studies at the station have changed just as the science and its practitioners have changed.

No account of Lawrence Blinks would be complete without telling about Anne Hof Blinks, who showed how much she and Lawrence enjoyed each other by teasing and making affectionate comments—she about his absentmindedness and how he would wander off into another subject when talking. She sat in on one of his plant physiology classes one summer, and during the course of the lecture and discussion, would tap her pencil on her desk and say, "Lawrence, we didn't cross that bridge with you." The students loved it, because he would look sheepish and own up that maybe it was a little confusing getting across. Mrs. Blinks had been a student at Radcliffe while Lawrence was a student at Harvard College (and the sexes were thus separated). She had become very interested in algae and used the Farlow Herbarium (at the Harvard end of Cambridge) to learn about them. Anne and Lawrence were married before he went to the Bermuda Biological Laboratory with W. J. V. Osterhout, so she enthusiastically went, too. They thoroughly enjoyed themselves in Bermuda, and named a species of *Halicystis*, a green alga from Bermuda after Professor Osterhout. *Halicystis* came to play an important part in the research of Lawrence in his days in Pacific Grove. Their son, John Blinks, was the apple of their eye.

Mrs. Blinks was a very talented weaver, and became an ethnographic specialist in tracing the evolution of designs used in weaving, from the common ones (for example, designs such as chevrons) to complicated ones. She grew sheep in their Monterey Peninsula "ranch" that were given names; we found it very amusing to be told we were eating part of "Brother" for dinner. It was always a special treat to be invited to dinner as Anne was a very creative cook. She wanted to have deep-brown wool to weave, and what better way to get a permanent dye than to have it grown for you.

She spent three weeks with my husband and me in Santiago, Chile, when we were there as visiting marine biologists one early spring. She had come along to see the weavings of the Andean Indians and spent most of her days visiting the National Museum as well as meeting some of the people who wove the items she was studying. She was also delighted with the pottery and leather goods that were found in the open markets; she was a wonderful guest to have along, because she was interested in so much, science as well as crafts.

My husband and I could not have been happier with them both in Pacific Grove for over 32 years.

L. R. BLINKS, A SCIENTIST DEDICATED TO EXPLORING PRINCIPLES OF PHYSIOLOGY

Throughout his career Lawrence Blinks was his own best salesman, through his short, well-organized publications. In his early career each paper tackled a particular part of the emerging puzzle for ionic relations for all cells. "The use of large coenocytic algae in the study of protoplasmic permeability and the accumulation of salts in the vacuolar sap has proved so valuable" (1927) in the world of 1920s biological research when the notion of cell permeability and specific regulation of ion movement by channels was still the faraway prize for physiology. This era of research had simple large-celled marine algae as model systems, well ahead of the giant squid axon of modern cell biology. Nonetheless, these early Osterhout and Blinks papers laid the foundation for modern neurophysiology. Blinks's contributions were as diverse as they were productive, with two dozen clearly written papers (nearly all of which were single author), 14 species of large-celled algae introduced as models (as reviewed by Blinks [1949, Table 1]) with a remarkable level of productivity, especially given the absence of NSF or other typical federal funding agencies for fundamental research in science for the first 20 years of his career.

Lawrence Rogers Blinks was born April 22, 1900, in Michigan City, Indiana, to Walter Moulton and Ella Little (Rogers) Blinks. He began as an excited naturalist during two summers spent at the University of Michigan's Douglas Lake research station after his freshman year at Kalamazoo College in 1919. He described himself as a frail child with limited chances to explore nature as a youngster. As a late teenager fascinated with the freshwater ecosystems and landscapes of Michigan, these field seasons must have been marvelous for Blinks, opening up to him the world of biology with courses in plant ecology and systematic botany. Blinks was profoundly affected by his time at Douglas Lake, electing to return to the region for a second year after finishing his sophomore year at Stanford University. The long-term effect of his Douglas Lake studies is shown by his use of new tools and technology to explore the plant species of the natural world across the latitudes—Bermuda, Dry Tortugas, and Pacific Grove. He collected his own materials for his experiments with morning treasure hunts looking for gifts from the sea for that day's experiment.

From Kalamazoo College in 1919 and Stanford University in 1921, L. R. Blinks was awarded a B.S. at Harvard University in 1923. He was awarded an M.A. from Harvard University in 1925 and a Ph.D. from Harvard in 1926.

Work conducted in Bermuda in 1924 as part of his graduate study with Osterhout was published a few years later (1928) and marked Blinks's entry into the manipulative phase of experimental electrophysiology. Researchers of that day had to produce their own fine capillary points to withdraw sap before injection of an experimental solution into cells. Method development and tinkering were an essential part of this period—each new alga studied, an essential part of the puzzle. Early efforts in replication certainly meet our current standards, with as many as 30 cells of a single alga being impaled before an interpretation could be rendered. Each new observation is met with critical evaluation: "Hence, as far as we can judge from these experiments, the protoplasm can tolerate a considerable amount of sulfate on the vacuolar as well as on the outer surface" (1928).

Blinks started work as a new Ph.D. at the Rockefeller Institute comparing algae across two *Valonia* species and a *Halicystis* species using clear graphics to document genus-specific differences in electrophysiology (1927, 1928). Blinks argues that the use of novel approaches such as newly measurable physiological features—differences in ions that make up the vacuolar sap in two near look-alikes—are not accidental and reveal species differences. He reasons that *Valonia macrophysa* "specific gravity is correlated with its sap content,...the solution of (chiefly) potassium chloride in the vacuole having a higher density than the sea water. This cell contrasts markedly with the other Bermuda coenocyte studied (*Halicystis*), the one known locally as 'sea bottles,' washed ashore during part of the year on exposed beaches of the south shore" (1927). These observational powers coupled with exploratory electrophysiology set Lawrence Blinks on a path to high levels of productivity and a lifetime of puzzles to be solved.

By age 49, with 20 single-author electrophysiology papers, he writes,

> The advantages of such multinucleate cells are several: they occur either singly, or easily separable from their neighbors…and they survive well in the laboratory, often for days or even weeks with a fine glass tube making connection with the cell sap. The large and measurable surface allows expression of resistance and capacity in definite terms; the capacity being often as high as several microfarads in a single cell, and resistances as high as one megohm (1949).

Further, of importance for an experimentalist is the realization that

> new solutions may be quickly applied over the whole surface, or at definitely separated areas…The cell sap may be analyzed for its constituents, or…may be replaced within the vacuole by perfusion with…other new solutions. Through these means effect of ionic and other changes has been studied at both the outer and inner (or vacuolar) protoplasmic surfaces, leading to a better understanding of the gradients, and the origin of the bioelectric potential (1949).

With these contributions Lawrence Blinks laid a substantial foundation for the 1963 Nobel Prize-winning work of Hodgkin (another Rockefeller fellow) and Huxley "for their discoveries concerning the ionic mechanisms involved in excitation and inhibition in the peripheral and central portions of the nerve cell membrane"(http://nobelprize.org/nobel_prizes/ medicine/laureates/1963/). On the occasion of Lawrence's 85th birthday, Hodgkin noted that he had "read all your papers on the large plant cells and had been particularly impressed with those dealing with the increase in membrane conductance during the activity of Nitella. This had a great effect on my scientific development as I have related in "Chance and Design" (a scientific autobiography of Hodgkin)" (Briggs et al., 1989).

THE PHOTOSYNTHESIS ERA

At the same time that Blinks's lifelong interest in physiology developed, researchers in a new discipline of physiology—photosynthesis—were also quickly gaining momentum. Blinks worked in the same research station (Hopkins Marine Station) or same faculty (Stanford) with some of the giants of early photosynthesis research: C. B. Van Niel, Stacy French, and other physiologists, such as A. C. Giese. Cross-fertilization likely enticed Blinks to enter this field, as important technological and biological issues were being explored in the late 1930s. One can argue that Lawrence Blinks's background in electrophysiology made him uniquely prepared to make several significant contributions to photosynthesis research.

While electrodes were commonplace in the study of gradients and bioelectrical potentials, the study of photosynthesis had not progressed past slow manometric methods as used by Emerson and other early photosynthesis researchers. Blinks's work had taught him that biological systems respond to stimuli (ion concentrations, light availability) on a timescale that his electrodes could detect (Blinks and Skow, 1938). Not surprisingly, he took this same technical approach to the study of oxygen evolution and pH changes in response to illumination. (It is interesting to note that Osterhout had taken a similar step in documenting induction phenomenon of photosynthesis in 1918, and is credited with interesting other Harvard undergrads, including Robert Emerson, in research in the area of photosynthesis.)

In the field of photosynthesis research Blinks's contributions used electrodes. Blinks used his technical electrode expertise and a vast variety of kelp forest plants at Hopkins Marine Station to his advantage (e.g., Blinks and Skow 1938). This important technical contribution has been mostly overlooked, with current electrodes taking advantage of modifications of Clark.

Among the three most important papers of this era was Blinks's joint work with Francis Haxo, where the relationship between absorbance and photosynthetic oxygen evolution was evaluated, again using the Blinks-style electrode (Haxo and Blinks, 1950). This work entailed painstakingly detailed measurements of absorbance using an integrating sphere and steady-state measurements of oxygen evolution as a function of specific wavelengths of light. To achieve this level of control for spectra, the entire Blinks lab was turned into a dark room with the monochromator irradiating entire tables, creating an unforgettable visual effect for those who passed by. With this 1950 publication green, brown, and red algae were compared using the best lamina available from the kelp forest diversity—another hallmark of Blinks's research. In sum, Blinks and Haxo contributed the first quantitative basis for relative absorption and oxygen evolution for nongreen plants, those that dominate coastal ecosystems.

Armed with state-of-the-art technology and with the kelp forest to explore, Blinks with Conrad Yocum demonstrated that the diversity of a kelp forest possesses "uniform efficiency of 0.08 molecules O_2 per absorbed quantum for (a) chlorophyll of one flowering plant, green algae, and brown algae, (b) fucoxanthol (fucoxanthin) and other carotenoids of brown algae, and (c) the phycobilin pigments phycocyanin and phycoerythrin of red algae" using his electrode and estimates of the relative absorption by these plants (1954).

With rapid response electrodes he was the first to detect chromatic transients, the first evidence of two reaction centers for photosynthesis (1957) with work conducted in 1955 and discussed at that international meeting. Despite crediting respiration as the likely explanation—a very appropriate line of thinking for a physiologist—Lawrence Blinks along with Caltech researcher and undergraduate friend Robert Emerson used marine algae to unlock the puzzle of how two light-harvesting systems functioned in photosynthesis through their paired discoveries of the Emerson effect and the Blinks effect (see Govindjee, 2006). In 1959 Blinks contributed a study of chromatic transients in *Ulva* photosynthesis, dedicated in memoriam, to Emerson. By 1960 Blinks's National Academy of Sciences publication extended this approach across algal lineages.

These publications provided the best understanding of photosynthesis by ocean plants for the next 50 years.

THE PHYSIOLOGICAL ERA OF MARINE ECOLOGY

Blinks's focus on physiological research, coupled with his synthesis pointing out high productivity in coastal ecosystems (1955) allowed many to realize the great growth potential exhibited by larger ocean plants, not just the unicells of early photosynthesis research. The Blinks 1955 publication was cited for over 40 years as a critical reference in the early years of marine ecology; his perspectives stimulated an emerging marine ecology discipline by drawing attention to the macroalgae in marine coastal environments. By providing a data-rich perspective, Blinks helped shape the developing marine ecology world, and extended the understanding of the role of photosynthesis in oceans and coastal plant communities. A festschrift on the occasion of his 85th birthday gathered researchers from across the nation and across these disciplines, to celebrate the career of L. R. Blinks. Few physiologists have had such reach, from electrophysiology to fundamentals of photosynthesis to laying a foundation for marine ecology—in one career.

By 1965 he was relieved to retire from his "benign dictatorship" as director of Hopkins Marine Station, and to return to his early love, bioelectrical phenomena of giant algal cells. Those days extended well into his late 80s, with joyful work puzzling out the relationships of these gems of the sea. His work began with daily hunts—walking along the foggy beaches of Carmel and Pacific Grove—for new *Halicystis* cells in the wash, and the promise of new chapters in electrophysiology.

LEADERSHIP TO SCIENCE AND SOCIETIES

Lawrence Blinks was an editor of the *Journal of Physiology* from September 1950 to July 1962. He was an editor or on the editorial board for *Annual Review of Plant Physiology, Biological Bulletin,* and *Botanica Marina.* He was recognized with the Stephen Hale Award by the American Society of Plant Biology in 1952 for his studies in photosynthesis and physiology of algae. Blinks was elected to the National Academy of Sciences in 1955, and served as assistant director of the National Science Foundation from 1954 to 1955. He was twice awarded a Guggenheim Fellowship and was awarded a Fullbright Scholarship in 1957 to work at Cambridge University, England. He held the position of visiting professor, University of California, Santa Cruz, from 1966 to 1972, during the formative years of that campus, and he contributed to the planning for the biological sciences departments there. Blinks was a fellow of the American Academy of Arts and Sciences, American Association for the Advancement of Science, California Academy of Sciences, Society of General Physiologists (president, 1952), and Western Society of Naturalists (president, 1950).

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