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The Cold Spring Harbor Phage Course (1945–1970): A 50th Anniversary Remembrance

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THIS year marks the 50th anniversary of the birth of the Cold Spring Harbor Phage Course and the 25th anniversary of its demise. The course was first taught in 1945 by MAX DELBRÜCK (with the assistance of A. H. DOERMANN and J. REYNOLDS) and last taught in 1970 by WILLIAM F. DOVE and RENÉ THOMAS. In its 25-year lifespan, the Phage Course was remarkably productive. Graduates included MARK ADAMS, MARTHA BAYLOR, SEYMOUR BENZER, ROBERT EDGAR, HERMAN KALCKAR, AARON NOVICK, FRANK STAHL, GUNTHER STENT, LEO SZILARD, NORTON ZINDER, and dozens of others whose names evoke pleasant and reverent memories of the infancy of molecular biology. The lifetime of the Phage Course coincided with a time when new ideas emerged almost as abundantly as new details, when students could be more or less familiar with the entire literature, and when field representatives from NIH frequently visited university campuses looking for ways to invest federal research funds.

The Phage Course was started by DELBRÜCK, whose missionary devotion to bacteriophage biology led to an explosion in the population of phage workers between 1940 and 1965 (LURIA 1966). The course was essential training for more than a generation of phage biologists. For some of us, it was truly an introductory course in which we learned the arts of sterile technique, serial dilution, soft agar plating, and plaque counting. For others, already skilled in basic microbiological methods, the Phage Course was a rite of passage through which ordinary microbiologists could become members of the Phage Group, a rather exclusive circle with DELBRÜCK at its center.

For DELBRÜCK, the only biology was "quantitative biology." It was not surprising, therefore, that his course for new phage workers was founded at the Cold Spring Harbor Laboratory of Quantitative Biology. Nor was it surprising that DELBRÜCK, who was trained as a physicist, looked to physics as a source of prospective quantitative biologists. He believed that the complexities of

biological systems might conceal new principles of physics and that the researchers most likely to discover these new principles were physicists. He actively sought converts, and among the most distinguished students of the Phage Course were a number of physicists, coaxed by DELBRÜCK to take a little taste of biology and discover how delicious it could be.

I took the Phage Course in 1957 at Caltech, which is about as far from the Long Island home of the Course as you can get in the contiguous United States. The precedent for teaching the Cold Spring Harbor Phage Course at remote sites was established early in its history. In 1949, for example, DELBRÜCK himself offered a cloned Phage Course at Caltech for a very small class, consisting of JEAN WEIGLE and OLE MAALØE (MAALØE 1966). When I took the course, it was taught by RENÉ COHEN, a French nuclear physicist recently turned phage geneticist, and FRANK STAHL, a postdoc in the phage group. COHEN was a teacher in the DELBRÜCK tradition, bringing to the course a convert's devotion and a physicist's rigor. I retain just two vivid recollections of discussions with COHEN: in one, he explained his aversion to the "sandveetch," which was a barbarism because it had to be eaten with the fingers; in the other, he explained why it would be impossible to manufacture an optical device that could scan a petri dish and count phage plaques. The other instructor, FRANK STAHL, was working with MESELSON on ways to test the idea that DNA synthesis was semi-conservative. My clearest memory of STAHL's teaching is a chalk-talk he gave on "mating theory," a mathematical analysis of recombination in phage. The theory had appeared first in a very difficult paper by VISCONTI and DELBRÜCK (1953)—a paper Stahl considered "one of the worst ever written"—and, together with CHARLEY STEINBERG, STAHL had reworked the old problem and produced a comparatively clear and lucid theory (STEINBERG and STAHL 1958). Standing at the blackboard and explaining the mathematics, STAHL did an imitation of

DELBRÜCK. I do not know if the imitation was calculated or unconscious, but the likeness was certainly evident to anyone who had seen DELBRÜCK lecture. The exposition moved slowly, interrupted by long pauses (eyes shut tight to show intense concentration), mumbled soliloquies, and sighs of satisfaction when the pieces finally fell into place. I have always loved the STEINBERG-STAHl solution to "mating theory," partly because STAHL gave it to us that day in 1957 as if it were a gift he had received directly from the gods. DELBRÜCK himself took little part in the course—he had turned his attention by that time to phototaxis in *Phycomyces*—but his office was just across the hall from the teaching lab, and he dropped in from time to time to offer encouragement.

The students in this class were, I believe, DENNIS BARRETT, JOHN CAIRNS, LEA SEKELY, ILGA LIELAUSIS, ANN ROLLER, EDWARD SIMON, BARBARA SUSMAN, and me. There is some dispute about ED SIMON's exact role in the course. LEA SEKELY says he was her lab partner at the beginning of the course, but that he dropped out soon after the course began. DENNIS BARRETT, BARBARA, and I also believe that SIMON was a member of the class, but SIMON himself says he did not take the course and suggests that he was simply a "groupie." We worked in pairs. My lab partner was ILGA LIELAUSIS, who at the time was the lead worker in the phage kitchen. She was a gifted lab worker who eventually became ROBERT EDGAR's co-author on a series of papers describing temperature-sensitive mutants of phage T4. Our experiments in the Phage Course always worked because ILGA did all the pipetting. My wife, BARBARA, who at the time was MATTHEW MESELSON's technician, was paired with DENNIS BARRETT, a biochemistry graduate student who is now an Associate Professor of Biology at the University of Denver. DENNIS loved folk songs and group dancing and instigated much of the social life of Caltech graduate students. I feel that I must record here an act of heroism for which DENNIS deserves to be remembered. A large group of us graduate students organized a picnic one summer on the beach at Playa del Rey, and DENNIS volunteered to shop for the food. Everyone but DENNIS showed up on time. We spent a long, hungry afternoon watching the planes from LAX take off over our heads and wondering why DENNIS and the hot dogs had not arrived. DENNIS finally appeared, laden with grocery bags and wrapped in bandages. He had purchased our provisions and then, bags in hand, had walked through a plate glass window of the grocery store. After visiting the Emergency Room and enduring over 100 stitches, conscientious DENNIS retrieved the bags of food from the grocery store and joined the picnic.

EDWARD SIMON is now a Professor of Biology at Purdue. He was one of several students in our class who decided to confirm the MESELSON-STAHl experiment

in organisms other than bacteria; ED showed with BrdU labeling that DNA synthesis was semi-conservative in HeLa cells. LEA SEKELY is now Program Director in the Chemical and Physical Carcinogenesis Program at NCI; her specific area of interest is hormonal carcinogenesis. ILGA LIELAUSIS retired from Caltech a few years ago. Unfortunately, I have not been able to trace ANN ROLLER.

Certainly the most sophisticated member of the class was JOHN CAIRNS. CAIRNS was already a well-known animal virologist. He had come to Caltech from Canberra for a four-month visit to learn from RENATO DULBECCO how to grow animal viruses in tissue culture. On discovering that the famous Cold Spring Harbor Phage Course was to be offered during that four months, CAIRNS decided to become a member of the class. He was good-looking, self-assured, spoke with an accent that was British rather than Australian, and had an innovative flair. He was admirably modest, generous and collegial, but he certainly stood out in our class. It was rather as if SIR LANCELOT had decided to attend the senior prom. JOHN and his partner, ANN ROLLER, did all the experiments with such ease that they could always manage to do something extra. It was ANN who shared the news with the class. "JOHN and I tried two higher multiplicities of infection to see if that affected the latent period." "JOHN and I think we found a few new plaque morphology mutants." Even within the confines of a scripted laboratory course, CAIRNS found ways to be original.

Graduation parties were part of the tradition of the Phage Course, probably because DELBRÜCK liked parties and looked for opportunities to arrange them (Figure 1). BARBARA and I missed the party celebrating our graduation from the Phage Course because she was pregnant and felt queasy that night. The party was at the Prufrock House—so called because it was discreetly listed in the Pasadena telephone directory under "J. A. PRUFROCK." The house was occupied by MATT MESELSON, HOWARD TEMIN, JAN DRAKE, CHARLEY STEINBERG, JOHN CAIRNS during his visit, and perhaps others whom I have forgotten. The next day, MESELSON, obviously shaken by the experience, told me about the party. The celebration began with organized silliness; for example, ILGA, blindfolded, had to use her toes to determine the agar content of the medium in several petri dishes, and ANN and JOHN had to step into a closet and recombine five of their "phenotypes" (articles of clothing) (Figure 2). The party ended with a water fight that drenched everything in the Prufrock House. The recipe for a Phage Course graduation celebration generally included generous quantities of agar, vodka, and water.

In 1960, I myself had a chance to teach the Phage Course at Cold Spring Harbor. ROBERT EDGAR was an Assistant Professor at Caltech at the time. CSH Director ARTHUR CHOVNICK invited EDGAR to teach the Phage

FIGURE 1.—The Board of Examiners at the Phage Course final examination and commencement exercises, held at the Prufrock House, Caltech, 1957. From the left: HARRY RUBIN, MAX DELBRÜCK, RENÉ COHEN, MATTHEW MESELSON, and FRANK STAHL. The person with his back to the camera may be HARRIS BERNSTEIN. (Photograph courtesy of DENNIS BARRETT, University of Denver.)

Course, and EDGAR offered me the opportunity to serve as his assistant. I decided this was a wonderful chance to get some teaching experience and accepted the invitation. For about five weeks that summer, I ate and slept in Blackford Hall at the Cold Spring Harbor Lab and spent most of every day with EDGAR, who was the most meticulous and conscientious of teachers. We pretested every experiment and did not give up until we could be almost certain that the experiment would work. In class, EDGAR was loud, eager, and vigilant. His pre-lab lectures were pep talks—simple, clear, well organized, and illustrated by poorly drawn diagrams with frequently misspelled labels. (The class skit featured EDGAR giving a spirited talk on the use of a spoon, which looked in the drawing like a butternut squash and was labeled “spone.”) He ran a group experiment as if he were a coach training a football team. He shouted out the time in kinetics experiments, strictly and noisily enforced the rules of sterile technique, endlessly circled the room to check that the surfaces of the soft-agar plates were smooth as glass. I did learn a lot about teaching that summer and, to the extent that my more timid personality allows it, I continue to imitate EDGAR when I teach students how to do a one-step growth experiment.

EDGAR taught the portion of the lab course that dealt with virulent phages, and ED LENNOX covered the temperate phages. I believe LENNOX arrived at the Lab only a few days before his section of the course began. I remember looking forward to meeting the ingenious fellow who had used the power of phage biology to demonstrate that individual antibody-producing cells could produce one, and only one, antibody. Since LENNOX was on the scene, I find it surprising that I was the

one who lectured on the kinetics of phage neutralization by antibodies. However, I remember vividly that I did give that lecture, since it was done impromptu during a class break, when EDGAR suddenly, and without prior notice, asked me if I could explain the mathematics of “one-hit” phage inactivation. Fortunately, he chose a topic that my Caltech training had prepared me to discuss. We were at the time deeply immersed in inactivation kinetics.

The able archivist at Cold Spring Harbor, CLARE BUNCE, has found the lists of instructors, students, and seminar speakers for every one of the Phage Courses from 1945 to 1970. The *only* records that have eluded the archivist’s investigatory skills are the ones for the summer of 1960, when I assisted EDGAR and LENNOX. My memories of that summer at Cold Spring Harbor have faded. We had roughly 20 students, and I spent a lot of time with them, but the only ones I can name with confidence are NOBORU SUEOKA, ULF HENNING, IRWIN RUBENSTEIN, and FRED FRANKEL. SUEOKA is memorable because he was such a gifted experimentalist and had such a sharp eye. For example, he could always spot the 0.2-ml pipette in the can of 0.1-ml pipettes or the pin-point colony on a supposedly sterile petri dish, and he let us know gently that we had to prepare materials more carefully if we wanted the experiments to work. Other members of the class have become indistinguishable in my mind from the dozens of people with whom I talked and ate and swam, summer after summer, at the annual Cold Spring Harbor Phage Meetings.

I recall two notable scientific discussions that I had with BOB EDGAR that summer. The first sticks in my mind because it turned out to have damaging relevance to my own work. When we first arrived at Cold Spring

FIGURE 2.—The Recombination Test, in which ANN ROLLER (left panel) was required to exchange five phenotypes (articles of clothing) with JOHN CAIRNS. When they emerged from the recombination closet (right panel), CAIRNS (left) was dressed as ROLLER, and ROLLER (right, with culture apparatus over her head) was dressed as CAIRNS. The gentleman in the derby hat in the left panel is DELBRÜCK; the gentleman in the beret and muffler in the right panel is RUBIN. (Photographs courtesy of DENNIS BARRETT, University of Denver.)

Harbor that summer, EDGAR met with GEORGE STREISINGER and discussed several experiments on which they might collaborate. One of these, EDGAR told me, was a mapping experiment to test for circularity of the linkage map of phage T4. This, EDGAR believed, was a long shot, but if *E. coli* could have a circular linkage map, why not T4? Their decision to test this unlikely hypothesis could not have come at a worse time for me. My thesis research at Caltech was aimed at determining the size of the mating group in T4 (*i.e.*, how many phage chromosomes could participate in a single crossover event). The experiment was based on the STEINBERG-STAHN mating theory, which in turn was based on the assumption that phage chromosomes were linear. While I was writing my Ph.D. thesis, STREISINGER, EDGAR, and GETTA HARRAR-DENHARDT (1964) were doing experiments that demonstrated the circularity of the T4 linkage map and simultaneously demolished the theoretical underpinnings of my thesis. The discovery that the map was circular was exciting in itself and led, over the next few years, to marvelous revelations about the

complex life cycle of phage T4 (see, for example, MOSIG 1983). For me, a graduate student working on the last draft of my Ph.D. thesis, the news that T4 had a circular map was worrisome. The Fates had arranged for me to defend my thesis dressed in the Emperor's new clothes! Fortunately, MAX was willing to let me get a degree on the basis of my suddenly obsolete work because he found my thesis interesting, and his sole test for an acceptable Ph.D. thesis was that it be "either interesting or original—not necessarily both." *Reality* was not on his list of criteria. After all, MAX never really believed any experimental demonstration of anything.

The second discussion I had with BOB EDGAR took place on the beach overlooking the outer harbor. I was sunning with BOB and his wife, LOIS GLASS EDGAR, when he told me that he had been thinking about changing directions in his research when we got back to Pasadena. He might give up studying the mechanisms of recombination in phage and start looking for a new class of mutants, mutants that were unable to grow at elevated temperatures. HOROWITZ AND LEUPOLD (1951)

had done experiments like that with *Neurospora* and *E. coli* and had shown that such mutations occurred in exactly the same genes that had already been identified by looking for other, more gene-specific phenotypes. The advantage of “temperature” mutations was that they were lethal only if the temperature was elevated. Why not try to isolate mutants like that in T4? BOB asked me to keep his plan a secret and, in particular, not to tell CHARLEY STEINBERG about it, because he was certain that CHARLEY would consider it ridiculous and would think of so many excellent reasons *not* to do the experiment that the project would be abandoned before the first plate was poured. Of course, BOB *did* do the mutant hunt when we got back to Caltech—in a locked room, safely out of CHARLEY STEINBERG’s ken—and the *ts* mutants became a treasure that BOB shared freely with the phage world (EDGAR and LIELAUSIS 1964).

The Phage Course of 1960 ended with the traditional commencement ceremony. The featured speaker for the Class of 1960 was the bombastic “DR. PLOTCHKISS,” played, of course, by ROLLIN D. HOTCHKISS, who himself had been a member of the very first phage class. DR. PLOTCHKISS wore, I believe, a mortar board over an abundant and unruly mass of hair. He carried an enormous, accordion-folded scroll of paper on which his “speech” was written. He delivered 10 or 15 minutes of loud, scholarly nonsense, and, as he spoke, his academic gown somehow fell open to reveal an impressive, spherical belly on which was painted a huge red target.

JOHN CAIRNS, who had been my classmate in the 1957 Phage Course, became the Director of the Cold Spring Harbor Lab and invited me to be the Instructor for the summer course in 1966. He asked me to suggest candidates for the second Instructor position, and I immediately named FRANCES WOMACK, who was at Vanderbilt University. I had never met FRANCES, but I was greatly impressed by her published work on the role of phage heterozygotes in recombination in phage T4. She had done single-burst experiments using so many closely linked markers that her resolution of recombination events seemed almost the equivalent of molecular sequencing (WOMACK 1963). Since DNA sequencing was not possible in 1966, FRANCES’ work seemed wonderful to me—a combination of brute strength and brilliant analysis. I figured that anyone with the patience and energy to do crosses involving nine markers or more could be counted on to carry more than a fair share of the work that needed to be done in teaching the Phage Course. I was right. FRANCES was a perfect partner for the job. She was smart, full of fun, and happy to take on big jobs. She was, however, hard to get started in the morning, and her son and daughter, who were up with the birds, would arouse FRANCES by serving her a breakfast of Coca Cola in bed.

FRANCES seemed to be fueled by Coca Cola and almost always had a bottle of it in her hand.

BARBARA and I and our two sons, then 4 and 8 years old, stayed in the Firehouse, which once housed the Cold Spring Harbor fire department. In 1930, it was moved by barge across the harbor to the grounds of the Biology Lab [and it has moved once more since we stayed in it (WATSON 1991)]. When RIC DAVERN, who was associate director of the Lab, showed us to our quarters, he seemed a bit apologetic, but we were comfortable in the small apartment, and the location was perfect. Right next door was Davenport Laboratory, where the Phage Course was taught; I could commute from home to work in two minutes, and so could my sons, who frequently came running into the lab while an experiment was in progress to announce exciting news of one sort or another. The class skit that summer made much of my older son’s appearance one day with a huge horseshoe crab that he had captured while it was spawning. The boys loved Cold Spring Harbor and seemed extraordinarily energized by the sea, the enormous grounds, the numerous places to climb and to hide. I have often thought that BOB HASELKORN and his family, who lived beneath us in the Firehouse, must have had mixed feelings about their accommodation that summer. They could hardly have failed to notice the stomping of the two little boys upstairs.

Here are the students in the class that FRANCES and I taught in 1966. I cannot resist offering this list because, like all teachers, I take pride in the accomplishments of my students. (The degrees and institutions shown on this list are copied from the original course roster.) ANDREW J. BECKER, Ph.D., Albert Einstein College of Medicine; FLORENCE CAHN, B.A., MIT; JOHN H. CASTER, B.S., St. Louis University School of Medicine; ANANDA M. CHAKRABARTY, Ph.D., University of Illinois-Urbana; STANLEY N. COHEN, M.D., Albert Einstein College of Medicine; DAVID B. FANKHAUSER, B.A., Johns Hopkins University; MARIA C. GANOZA, Ph.D., NIH; MAX E. GOTTESMAN, Ph.D., The Rockefeller University; THEODORE GURNEY, JR., Ph.D., MIT; JOST KEMPER, Ph.D., Cold Spring Harbor Laboratory of Quantitative Biology; STANLEY P. LIEBO, Ph.D., Oak Ridge National Laboratory; DANIEL H. LEVIN, Ph.D., Lab of Biophysics, Beth Israel Medical Center; LEON J. LEWANDOWSKI, B.S., Wistar Institute; CARL R. MERRIL, M.D., NIH; WIM J. MÖLLER, Ph.D., Johns Hopkins University School of Medicine; HAROLD C. NEU, M.D., Columbia University College of Physicians and Surgeons; JOHN W. QUIGLEY, M.S., Rutgers University; WOOLLCOTT K. SMITH, M.S., Johns Hopkins University; HIROKO WATANABE, M.D., Royal Victoria Hospital, Montreal; ROBERT YUAN, B.S., Albert Einstein College of Medicine.

Readers will, of course, recognize many names on this list. It was, like all the other Phage Course classes, a collection of gifted people. Yet many of them had

never flamed a pipette, isolated a bacterial colony, or seen a phage plaque. A few members of the class were unfamiliar with semi-log graph paper, and we had to explain to them how and why such paper is used. FRANCES taught them to recognize plaques arising from phage HETs (single phage particles that give rise to a mixed progeny of r and r^+ phages). She explained how to do spot tests for complementation and recombination of rII mutants; she herself had done zillions of such tests. We did a big single-burst experiment, another of FRANCES' specialties. I prepared the class for experiments that required mathematics—serum inactivation, UV inactivation, nitrous acid induction of mutations, and mapping. The math was essentially the same for most of the labs; only the notation changed. In addition, I tried, probably unsuccessfully, to get the class excited about the STEINBERG-STAHN mating theory. And, following the DELBRÜCK tradition, I derived the Poisson distribution for the class. One cannot do phage biology without the Poisson distribution. Like MAX, I mischievously used a tank of tiny fish to illustrate the derivation, thus creating an uncertainty in the minds of my listeners concerning the origin of the “poisson” in the name of the distribution.

I will mention here only two of the students in this engaging and brilliant class. STAN COHEN stood out because he was so busily involved in a research project that was in progress at Einstein. He made two or three phone calls a day from the wall phone on the South wall of the Davenport Lab. He scribbled numbers on his note pad, gave urgent instructions for the next experiment, and always set up the time for the next contact. FRANCES and I wondered why he had come to Cold Spring Harbor when he was so intensely concerned about work that was going on elsewhere. He was, however, an apt student and seemed genuinely interested in the work he was doing in our course. I remember ANANDA CHAKRABARTY because he seemed so interested in working on exotic organisms that grew on odd substrates and smelled bad. Why would you want to work on organisms that ate asphalt when you had access to well-behaved organisms that ate carbohydrates?

Students participating in the Phage Course carried home a great deal more than a handful of useful techniques. They felt that they had been initiated into the community of biologists. The course featured seminars by leaders in the field, and the students could sit and drink beer with them on the porch at Blackford Hall or chat with them on the beach. When FRANCES and I taught the course, the seminar series included talks by C. A. THOMAS, F. FRANKEL, D. J. MCCORQUODALE, R. HASELKORN, A. SKALKA, C. RADDING, E. KELLENBERGER, E. GOLDBERG, J. KARAM, G. MOSIG, and R. S. EDGAR. It was worth a student's trip to Cold Spring

Harbor just to meet the scientists who worked year round in the labs there; that included BARBARA MCCLINTOCK and AL HERSHEY. I remember with special fondness PAUL MARGOLIN, who showed me the elaborate model train layout that he constructed during the winter months, when the social life at Cold Spring Harbor went into hibernation. In the summer, students could spend their evenings talking molecular biology with JIM WATSON, GEORGE STREISINGER, MAURICE FOX, and a host of other visitors who were drawn to the place year after year.

The pleasures of Cold Spring Harbor come not only from the science, which is wonderful, but also from the place, which is enchanting. The rhythm of the Phage Course often fell into harmony with the rhythm of the sea. We would schedule labs in the very early morning in order to be able to dig clams in the afternoon. On a hot day, when the beach was especially inviting, we would delay an experiment until late afternoon and head for the outer harbor. I remember one night when BOB EDGAR hunted me down and took me to the water's edge. A school of bioluminescent ctenophores surrounded the boat dock in the inner harbor. I scooped one of them into my palm. That simple blob of a creature has stuck in my memory; it was one of the most beautiful things I have ever seen. That is what the Phage Course and Cold Spring Harbor are all about—the wonder and the elegance of life.

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