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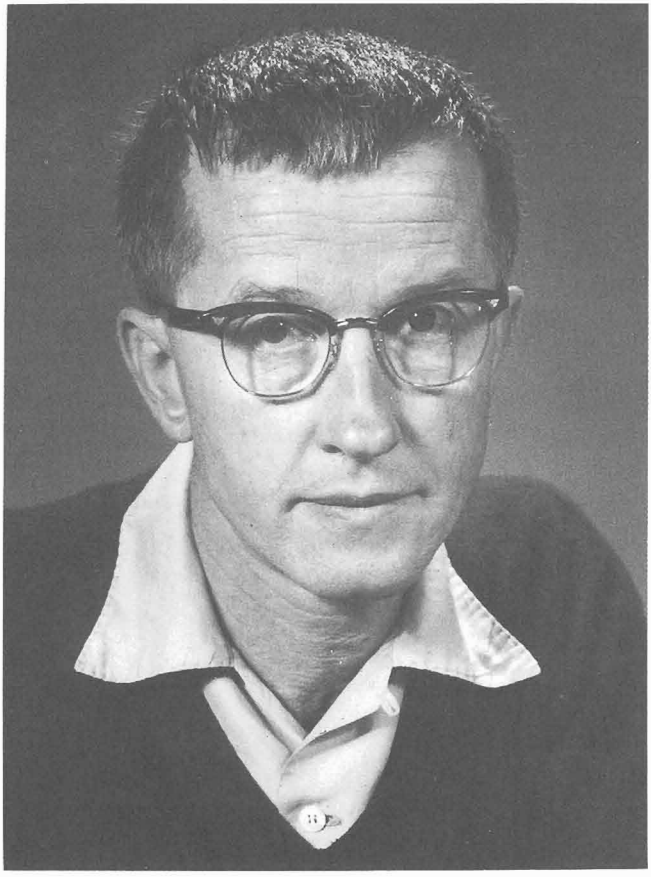
MAX LUDWIG HENNING DELBRÜCK

1906—1981

A Biographical Memoir by

WILLIAM HAYES

Biographical Memoir



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Max Delbrück

MAX LUDWIG HENNING DELBRÜCK

September 4, 1906–March 10, 1981

BY WILLIAM HAYES

MAX DELBRÜCK, or just Max as he was called by all his associates, was one of the outstanding natural scientists of our time. A man of rare intellectual ability, and clarity of thought and perception, he excelled in theoretical physics, biology, and philosophy, and possessed a deep knowledge and appreciation of the arts. His dedication to truth, and his intolerance of half-truths and intellectual pretension, were sometimes expressed with a disturbing frankness and abruptness of manner, often construed as arrogance by those who did not know him well. His disclaimer, "I don't believe a word of it," when told of some new experimental result or hypothesis, became famous among his colleagues. In fact, Max was very gregarious and had a rich vein of friendship and affection in his nature which he was always ready to share with others of all ages.

Above all, Max was a born leader whose Socratic influence on those who worked with him was enormous, whose rare praise was something to be coveted and remembered, and whose criticism was welcomed with respect; although

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he was often wrong in his scientific judgement, he was always the first to admit it. On a personal level he engendered in the minds of his friends and colleagues a deep respect and affection that they will not forget.

Max was the foremost pioneer of a new approach to an understanding of fundamental biological processes, now known as molecular biology. His most significant studies concerned the multiplication in their host cells of bacterial viruses, called bacteriophages or phages for short. These tiny particles are made up of about equal parts of two chemical components, protein and nucleic acid; infection of a bacterium by a single particle is followed, about 30 minutes later, by rupture of the cell and liberation of a hundred or more progeny particles. As long ago as 1922 the American geneticist H. J. Muller had suggested phage as the simplest possible model for studying the nature and behaviour of genes.

For their novel and important studies in this field, Max and his colleagues, Salvador Luria and Alfred Hershey, were awarded the Nobel Prize in Physiology or Medicine in 1969. However, no account of Max's published work can do justice to his overall influence as the leader of a formidable group of workers, many of them physicists like himself, who infused a new way of thinking, and a new life, into biological research. In addition, he was a direct source of encouragement and inspiration to young research workers of many nationalities and from many disciplines who came to work with him on bacteriophage at the California Institute of Technology, in Pasadena, California, or to attend his famous "Phage Course" at the Cold Spring Harbor Laboratory, Long Island, New York, and to whom his intellectual approach to biological problems became an inspiration for their own thinking.

FAMILY BACKGROUND

Max grew up in the Grunewald suburb of Berlin, the youngest of seven children (four girls and three boys) of an extremely prominent academic family. His father, Hans Delbrück, who was 58 years older than Max, was Professor of History at Berlin University, specializing in the history of the art of war, as well as sole editor for at least 30 years of a monthly journal, *Preussische Jahrbücher*, for which he wrote a column commenting on German politics. Three of his father's first cousins were, respectively, Professor of German Literature at Jena, Chief Justice of the Imperial Supreme Court, and Minister of State. His maternal great-grandfather was the famous Justus von Liebig, Professor of Chemistry at Giessen and Münich, Foreign Member of the Royal Society, and Copley Medalist.

His mother's brother-in-law, Adolf von Harnack, was Professor of Theology at Berlin University and a church historian; he was also Director of the Prussian State Library and, in 1910, became co-founder and President of the Kaiser-Wilhelm-Gesellschaft. The Harnacks, the Delbrück's nearest relatives, were also a large family and lived next door, while Karl Bonhoeffer, a Professor of Psychiatry, and his family were around the corner and the Max Planck family not far away. One of the Bonhoeffer sons, Klaus, married Max Delbrück's sister Emmie.

Max's family enjoyed "a modest degree of affluence and apparently the life until 1914 was pretty free and very hospitable. As war came and life became more and more of a nightmare in every respect, of course all this darkened. . . . I think three-quarters of the young men in the family [including his eldest brother] were killed. So that was all very sad, and in addition then there came these pretty severe food and coal shortages and then the total mess in 1918.

So this relatively affluent residential suburb after the war became almost a ghost town" (1).

World War II also brought tragedy to the Delbrück family. Two Bonhoeffer brothers, Klaus (Max's brother-in-law) and Pastor Dietrich, two Bonhoeffer sons-in-law, and two von Harnack cousins, Ernst and Arvid, together with the latter's American wife, were executed by the Nazis as leading members of the Resistance. Max's brother Justus was imprisoned by the Nazis, and liberated after the fall of Berlin but ten days later was arrested by the Russians and died in a diphtheria epidemic in a Russian camp. The husbands of two of Max's sisters also were killed by marauding soldiers in the last days of the war.

EARLY INTEREST IN SCIENCE

Of all the many children in the Delbrück, Harnack and Bonhoeffer families, Max was the youngest. Moreover, none of his intimates, save one, had any knowledge of, or interest in, science. The exception was Karl Friedrich Bonhoeffer, 8 years his senior, who became a distinguished physical chemist and Max's mentor and lifelong friend. Max's main boyhood interests were astronomy and mathematics. In retrospect, some 40 years later, he considered that he chose astronomy as a means of finding and establishing his own identity in an intimate society of so many able and strong personalities, all of them older than himself; but only he was an astronomer, and proclaimed himself one during his last 2–3 years at the Grunewald Gymnasium. He read popular books on the subject, was the enthusiastic possessor of a 2-inch telescope, and sometimes woke the whole household with the loudest of alarm clocks in the small hours of the morning when he had an appointment with the stars! (1) Despite Max's nuisance value, his parents proved tolerant and even helpful, while his

knowledge of astronomy blossomed under the tutelage and friendship of Karl Friedrich Bonhoeffer.

It thus became Max's intention to study astronomy at the university. In 1924, at the age of 17½, he went first to Tübingen where Hans Rosenberg offered an introduction to astrophysics which was then in its infancy; he also took courses in mathematics and physics, but chemistry failed to attract him and he never learned this subject as a student. He spent only one semester at Tübingen and then moved for a semester to Berlin where he had free tuition because of his father's professorship there, and thence to Bonn and back to Berlin again until, in the summer of 1926, he finally settled at Göttingen for 3 years until he obtained his degree.

Although Göttingen was at that time the center of excitement in theoretical physics, following Heisenberg's discovery of quantum mechanics in 1925, Max continued to be interested in astronomy and mathematics until his attempt to write a Ph.D. thesis on novae failed because, he admitted, the mathematics of astrophysical theory of the interior of stars was beyond him, while the relevant literature was in English which he did not know at the time. But in the effort he had had to learn a good deal of quantum mechanics which brought him into contact with some of the theoretical physicists, among them Max Born, Pasqual Jordan, Eugene Wigner and Walter Heitler.

At this time he wrote a short paper (1929) providing formal mathematical proofs for a theorem that Wigner had used in the application of group theory to theoretical physics. Born, who was Professor of Theoretical Physics, thereupon offered Max a Teaching Assistantship, and Heitler suggested that he extend to lithium the quantum mechanical theory of the homopolar bond that had just been developed for

hydrogen by Heitler and London. His conclusion was that the bond energy in Li_2 is considerably smaller than in H_2, not because of the repulsion of the K shells but because the bond electrons were two s electrons (1930a). Max recently averred that this topic turned out to be a nightmare for him because of the complexity of the mathematics involved and that he had never dared to look at his thesis again (1); but nevertheless it won him his Ph.D. Degree in 1930.

EARLY CAREER IN PHYSICS (1929–32)

Bristol

John E. Lennard-Jones, Professor of Theoretical Physics at the new H. H. Wills Physics Laboratory, University of Bristol, England, spent some months at Göttingen in 1929 and was anxious to attract to Bristol two of Max Born's students for whom research grants had been provided. Gerhard Herzberg, then a postdoctoral Fellow, and Max Delbrück were appointed. Max remained at Bristol for 18 months and became very friendly with Cecil F. Powell, with whom he roomed. Among other friends at that time were P. M. S. Blackett, later to become President of the Royal Society, P. A. M. Dirac and H. W. P. Skinner. Of these early associates four were later to win Nobel Prizes, three in physics (Dirac, Blackett and Powell) and one in chemistry (Herzberg).

An unpublished history of the Bristol Department, written by the late Professor A. M. Tyndall, related that "M. Delbrück, Prussian by birth but cosmopolitan by nature, a theoretical physicist recommended by M. Born, brought with him intellectual stimulus, critical judgement and social entertainment which gave help and pleasure to many and sundry." Another member of the department at the time, who remembers him quite well (J. Burrow, quoted by

N.T.)* describes him as a cheerful, outgoing person and one who rapidly established a reputation as a theoretician who was always ready to discuss problems of any kind with experimentalists who needed help and advice. Herzberg also recalled that he "fitted in very well with the group of younger physicists there because of his (then) gregarious ways and the ease with which he made friends." Max published two papers from Bristol in English (1930b; 1932), on topics related to the quantum mechanical theory of homopolar bonding on which he had written his thesis.

Copenhagen and Zürich

Following his Bristol experience, Max obtained a Rockefeller Fellowship (Physics) to study with Niels Bohr in Copenhagen where he spent the spring and summer of 1931, and then spent the last 6 months with another quantum physicist, Wolfgang Pauli, in Zürich. In Copenhagen he roomed, and collaborated on a nuclear physics project, with George Gamow (1931) with whom he established a lasting friendship. Also working with Bohr at that time was Victor Weisskopf, a very close friend since their student days together at Göttingen; they arrived in the United States almost simultaneously in 1937 (*see below*) and remained in personal contact until Max's death.

Anyone who might infer from all this that life in Copenhagen was a staid and serious business should read Max's lighthearted and facetious account of the gaiety and practical jokes of those days, in his contribution to a George Gamow Memorial Volume (1972c). Weisskopf (pers. comm.) has commented on his wonderful sense of humor: "There was a custom in Copenhagen, at each of the early conferences

*The initials in the text that indicate the source of quotations are explained in the acknowlegements at the end of the memoir.

organized by Niels Bohr, to have what we called a session of 'comic physics.' It was always Max who was the most spirited leader in these activities with his humour and intellectual fantasy. You must have heard of his rewriting of Goethe's Faust to make fun of the physics of that time."

Max's short visit to Copenhagen became of greater importance to him than he could have imagined, for it marked the turning point in his life that changed not only his career but his philosophical outlook as well. The determining influence was Bohr's formulation of the complementarity concept as a generalized extension of Heisenberg's uncertainty principle. Thus, the propagation of light may be unambiguously defined, in a probabilistic way, either as a continuous motion of electromagnetic waves or as the exchange of individual quanta of energy related to the wavelength of the former by Planck's constant, but not by both at the same time; the two expressions of reality stand in a mutually exclusive but *complementary* relation to one another. According to Max,

> Bohr then very vigorously asked the question whether this new dialectic wouldn't be important also in other aspects of science. He talked about that a lot, especially in relation to biology, in discussing the relation between life on the one hand, and physics and chemistry on the other—whether there wasn't an experimental mutual exclusion, so that you could look at a living organisim either as a living organism or as a jumble of molecules; . . . you could make observations that tell you where the molecules are, *or* you could make observations that tell you how the animal behaves, but there might well exist a mutually exclusive feature, analogous to the one found in atomic physics . . . in many respects Bohr wasn't sufficiently familiar with the status of the science (biology). So it was intriguing and annoying at the same time.
>
> It was sufficiently intriguing for me, though, to decide to look more deeply, specifically into the relation of atomic physics and biology—and that means learn some biology"(1).

Much has been written of Bohr's profound influence on Max. Thus, Gunther Stent writes, "I think it is fair to say that with Max, Bohr found his most influential philosophical disciple outside the domain of physics, in that through Max, Bohr provided one of the intellectual fountainheads for the development of 20th century biology" (3). Again, Horace Judson said of Max, "His mind and style had been formed by Niels Bohr, the physicist, philosopher, poet and incessant Socratic questioner who made Copenhagen one of the capital cities of science between the wars" (4, p. 50). But Max himself saw more than this in the so-called Copenhagen Spirit, as shown by his reply to a question about the Phage Group: "Well, the phage group wasn't much of a group. I mean it was a group only in the sense that we all communicated with each other. And that the spirit was—open. This was copied straight from Copenhagen, and the circle around Bohr, so far as I was concerned. In that the first principle had to be openness. That you tell each other what you are doing and thinking. And that you don't care who—has the priority" (4, p. 61).

It followed that, after a further 6 months with Lennard-Jones at Bristol, Max decided to accept an appointment as assistant to Lise Meitner at the Kaiser Wilhelm Institute for Chemistry in Berlin in the autumn of 1932, because of its proximity to the Kaiser Wilhelm Institute for Biology. But before returning to Berlin he paid a short visit to Copenhagen to hear Bohr deliver his famous address, "Light and Life," to the opening meeting of the International Congress on Light Therapy in August, in which he explicitly stated his views on complementarity in biology (9). Odd though these views may seem to us now, in retrospect, this lecture confirmed Max's decision to turn to biology.

THE BERLIN YEARS (1932–37)

Max's appointment as assistant to Lise Meitner, who was collaborating with Otto Hahn on the results of irradiating uranium with neutrons, was, in effect, to be a consultant on theoretical physics. During this period he did write a few papers, one of which turned out to be an important contribution on the scattering of gamma rays by a Coulomb field due to polarization of the vacuum produced by that field (1933). His conclusion proved to be theoretically sound but inapplicable to the case in point, but 20 years later Hans Bethe confirmed the phenomenon and named it "Delbrück scattering." A second seminal paper with Gert Molière, which Max referred to retrospectively as "very *learned*" (1), attempted to apply quantum mechanics to resolve the paradox of irreversibility in statistical mechanics (1936c).

Not long after the beginning of Max's Berlin period, which coincided with Hitler's rise to power, he organized a private group of five or six theoretical physicists to join in fairly regular discussions among themselves, often at his mother's house. At his suggestion some biochemists and biologists also joined the group. Among these were K. G. Zimmer whose interest was the dose effect of ionizing radiation on biological systems, and, most significantly for Max's future, N. W. Timoféeff-Ressovsky, a Russian geneticist from the Kaiser Wilhelm Institute for Brain Research who had been collaborating with Zimmer on the genetic effects of radiation for some 2 years before contact with Max was established. Timoféeff-Ressovsky's experimental organism was *Drosophila*, the fruit fly, which was then, and still is, very popular with geneticists because of its short generation time and the large populations that can be raised in the laboratory.

Zimmer records that he remembers vividly the discussion that followed: "Two or three times a week we met, mostly in Timoféeff-Ressovsky's home in Berlin, where we talked for ten hours or more without a break, taking some food during the session. There is no way of judging who learned most by this exchange of ideas, knowledge and experience, but it is a fact that after some months Delbrück was so deeply interested in quantitative biology, and particularly in genetics, that he stayed in this field permanently" (2, p. 33).

The upshot of all these discussions was a paper by Timoféeff-Ressovsky, Zimmer, and Delbrück (1935b) on the nature of gene mutation and gene structure, in which Max was mainly responsible for the theoretical interpretation. He supposed that the molecules from which genes are made must have a very unusual atomic constitution, since they show such remarkable stability in a cellular environment otherwise subject to constant chemical change. This stability suggested that each atom of the gene molecule is fixed in its mean position and electronic state by being sunk in "energy wells," so that discontinuous changes in their state, expressed as mutations, could arise only by the acquisition of very high energies such as ionizing radiations would impose (18, p. 26).

It is difficult to say how much interest this paper aroused at the time. Max reported that it got "a funeral first class" (1) since it was published in a little-known Göttingen journal, but Timoféeff-Ressovsky must have sent reprints to many geneticists although it is unlikely that they would have known enough physics to understand it. It was not until ten years later that the paper became famous through the publication in 1945 of Erwin Schrödinger's little book, *What Is Life?*, in which he maintained that Delbrück's model of the gene was the only possible one, and went on to put

forward the romantic and paradoxical idea, first proposed by Bohr, that "from Delbrück's picture of the hereditary substance it emerges that living matter, while not eluding the 'laws of physics' as established up to date, is likely to involve hitherto unknown 'other laws of physics' which, however, once they have been revealed, will form just as integral a part of this science as the former" (16). Max, of course, was already long embarked on his quest for this Holy Grail, but Schrödinger's book was influential in attracting into biology many physicists, curious to solve the paradox (see Stent, 2, p. 3).

Meanwhile, when Max was spending all this time immersed in biophysics, Hahn and Meitner's work on the irradiation of uranium with neutrons was revealing the emission of many characterizable transuranium products that were interpreted as elements, but their number then became so large that they were assumed to be isomers of transuraniums, and Max went along with this. As he admitted (1), ". . . this was really immensely stupid of me; I should have guessed what was really going on, namely fission, but I, like everybody else, lacked imagination to see that . . . it was something any experimental physicist could easily have figured out . . . all you needed to know was that there was excess energy there; the neutron enters and there is enough energy there to blow the nucleus to pieces. You needed to just be able to add and subtract . . . and it didn't occur to anybody until they were literally forced to this conclusion only the year after I left."

Max's decision to visit the U.S.A. was prompted by three circumstances. One was his now dominant interest in quantitative biology and especially in *Drosophila* genetics, which he wished to experience first hand. Then, a few years after becoming Lise Meitner's assistant, he had considered a future as a lecturer at the university, but, apart from aca-

demic criteria, this entailed certification of "political maturity" following participation in "free discussion" groups at a Nazi indoctrination camp. His failure to display sufficient "maturity" at two sessions, probably as a result of too much frankness, made it clear that a university career would not be open to him in the foreseeable future. Finally, in 1937 the Rockefeller Foundation offered him an unsolicited Fellowship (Biology) to travel abroad, so he took this opportunity to visit the California Institute of Technology in order to learn *Drosophila* genetics from Thomas Hunt Morgan and his world-famous group.

THE BACTERIOPHAGE EPOCH (1937–53)

Early Days at Caltech

Max's initial introduction to Caltech was frustrating and disappointing, despite the help of A. H. Sturtevant, and Calvin Bridges with whom he was especially friendly, he found the highly specialized *Drosophila* jargon too difficult and exacting to grasp, let alone master, in a reasonable time. One day he inadvertently failed to attend a seminar on bacteriophages by Emory Ellis, and went to him to find out what he had missed: "I had vaguely heard about viruses and bacteriophages, and I had read the paper by Wendell M. Stanely on the crystallization of tobacco mosaic virus before I had left Germany. I had sort of the vaguest notions that viruses might be an interesting experimental object for a study of reproduction at a basic level" (1). Ellis showed him the very rudimentary materials and the simple techniques needed for his experiments, and Max saw for the first time the small macroscopic areas of clearing, or plaques, on a lawn of bacterial growth on solid culture medium, each plaque representing the multiplication of a single virus particle. Ellis also demonstrated

some step-growth curves revealing the kinetics of a cycle of phage multiplication in newly infected bacterial populations. According to Ellis, Max's first comment was, "I don't believe it" (2, p. 53); but Max's own recollection was, "This seemed to me just beyond my wildest dreams of doing simple experiments on something like atoms in biology [which perhaps means the same thing!], and I asked him whether I could join him in his work, and he was very kind and invited me to do so" (1).

So began what has been called "The Phage Renaissance." Before this, d'Hérelle's initial studies demonstrating the particulate and viral nature of phage had been followed by the highly original investigations of F. M. (later Sir Macfarlane) Burnet and Martin Schlesinger, which laid the foundation of modern phage research, but Schlesinger died prematurely in 1936 and Burnet changed his field shortly afterwards; neither left disciples to carry on their pioneering mission. Moreover, after working for a year with Max, Ellis returned to his original work on malignant tumors of mice. So Max was left alone, and alone was responsible for giving continuity to phage research by founding and guiding an expanding, if loosely knit, lineage of phage workers that sowed the seeds that finally blossomed into modern molecular biology (see 5).

One of Max's first contributions, in his early days with Ellis, was to bring his analytical approach and mathematical knowledge to bear on study of the phage life cycle. For example, formulae were devised to check the rate of adsorption of free phage to bacteria under various experimental conditions, while the then unknown proportion of free particles able to produce plaques (the plating efficiency) was assessed by the application of Poisson's statistics of random sampling. In their only paper together, Ellis and Delbrück (1939) invented and greatly refined the

one-step growth curve and devised the single-burst experiment, anticipated in essence by Burnet, which permitted a comparison of phage multiplication in individual cells, both key methods for the future progress of phage research. Of this and two other papers by Max on the same topics (1940c,d). T. F. Anderson wrote 16 years later that, of the many scientific papers he must have read at the time, he could remember only these three: "The experiments were beautifully designed and reported in an elegant style that was new to me. The three papers carrying the Delbrück label formed a little green island of logic in the mud-flat of conflicting reports, groundless speculations, and heated but pointless polemics that surrounded the Twort-D'Hérelle phenomenon" (2, p. 63).

Max had no difficulty renewing his Fellowship for a future year, and when this extension expired the war had started so that a return to his old job in Berlin, which had been guaranteed by Hahn and Meitner, was virtually impossible even had he wanted it. On the advice of the Rockefeller Foundation he accepted a lowly academic position of Instructor of Physics at Vanderbilt University, Nashville, Tennessee, where he remained from 1940 until 1947, being finally promoted to Associate Professor. However, the Foundation, with generous foresight, agreed with the university to pay half his salary on the condition that half his time was free for biological research.

Vanderbilt University and the Phage Group

Max had no students of biology at Vanderbilt and his only recruit there was A. H. Doermann who had just obtained his doctorate in Neurospora genetics and later became a prominent phage worker. At the end of 1940, Max met Salvador Luria, a recent Italian refugee from Europe, who was working on phage at the College of Physicians

and Surgeons in New York. As Luria remarked 25 years later, "We were probably the only two people interested in phage from the point of view of molecular biology." They arranged to collaborate in experiments with mixed infections by phages T1 and T2 in the summer of 1941 at Cold Spring Harbor where Max was to read a paper at the annual symposium. In August that year Max married Mary (Manny) Adeline Bruce whom he had met during his fellowship at Caltech. The marriage took place in Pasadena and Manny has related that "Max took a whole week off from his experiments to get married. He couldn't wait to get back to Cold Spring Harbor" (7) where they spent their honeymoon.

For the mixed infection experiments Luria had isolated bacterial indicator strains, separately resistant to each of the two phages, and when he visited Max in Nashville a year later they began to discuss the problem of whether resistance arose by the adaptation of a constant small proportion of bacteria, induced by contact with the phage, or by spontaneous mutation. The obstacle to direct experimentation was that the only way to demonstrate resistance was by exposing the culture to the phage. It was Luria who first conceived the idea of comparing the numbers of resistant bacteria arising in otherwise identical *independent* cultures, initially seeded with only a few sensitive cells, with the numbers from equivalent samples from a single culture. If resistance was induced by contact with the phage, then variation in the numbers of resistant cells would, in either case, be within the limits expected by random sampling. In contrast, the occurrence of resistant *mutants*, which might arise spontaneously and begin to multiply at any time during the growth of each independent culture, would lead to a much wider variation. By this reasoning, a fluctuation greater than the sampling error, in the numbers of resistant bacteria from independent cultures, means that

these variants arose as clones in the cultures before they were exposed to the phage and, therefore, were mutants.

Luria wrote to Max about his idea and two weeks later Max provided the manuscript of a fully worked-out mathematical theory as a basis for experiments. The experiments showed unambiguously that bacteria acquire resistance to phage by mutation, a finding which has subsequently been established by virtually all other bacterial variations.

The paper by Luria and Delbrück (1943a) reporting their findings and conclusions is a landmark in the history of molecular biology, for it provided the first real evidence that bacterial inheritance, like that of the cells of higher organisms, is mediated by genes and not by some Lamarckian mechanism of adaptation as was widely held at the time. Thus, it signaled the birth of bacterial genetics which became a basic tool for exploring the molecular basis of life. Indeed publication of this paper has been compared in importance to that of Mendel in 1865, ushering in the science of genetics itself (4, p. 56). At about the same time, in Nashville, Salvador Luria initiated his studies of host-range mutations in phage, but these were not completed until later and were published in 1945.

Max and Luria had become interested in some papers on phage by Alfred H. Hershey, a microbiologist at the Medical School of Washington University, in St. Louis, and at the beginning of 1943 Max invited him to Nashville for a few days and wrote to Luria about him. Then, at the end of the year, Luria gave a seminar at St. Louis which "had the good fortune of impressing Hershey with the remarkable possibilities of phage genetics" (2, p. 173). These three formed the nucleus of the Phage Group consisting, as Max quipped, of two enemy aliens "and another misfit in society" because of Hershey's liking for independence and solitude (4, p. 53).

In addition, an important collaboration was established in the early 1940s with the electron microscopist Thomas F. Anderson. The basic aim of the Group was to understand the mechanism of phage replication—how infection by a single particle resulted in the liberation of some 200 particles half an hour later—and, of course, the nature of the gene.

It is not my intention in this memoir to recount the many ideas and experiments which followed their zigzag course toward the solution of these problems, which may be culled from the titles in Max's bibliography, but rather to show Max's overall involvement and influence on this enterprise. However, one important technical decision should be mentioned. Until 1944 most workers used phage strains and bacterial hosts which they themselves had isolated, so that it was almost impossible to build up a body of comparable knowledge. Max therefore negotiated a "phage treaty" under which it was agreed that research be concentrated on a set of seven phages (T1–T7), all of which infected the same host, *Escherichia coli* strain B.

Cold Spring Harbor and the Phage and Phycomyces Courses

After their first visit in 1941, Max and Manny returned to the Cold Spring Harbor Laboratory for the summer months nearly every year. They were often joined by Salvador Luria, A. H. Doermann, A. D. Hershey, Mark Adams and many others over the years who became interested in phage, not only for research but, more importantly, for intellectual interaction and stimulus. In 1950 Hershey became a member of the Department of Genetics of the Carnegie Institution of Washington, which was also located at Cold Spring Harbor.

In 1945 Max organized the first of 26 successive annual Phage Courses at Cold Spring Harbor, and was the princi-

pal instructor in the first three of them. This was made possible through the vision and enterprise of Milislav Demerec, director of the Laboratory from 1941 to 1960. Demerec was a classical geneticist who foresaw the potential of bacteria and their phages as genetic tools, abandoned *Drosophila* to work with them, and helped others to do the same. The course was devised not only for biologists but also for biochemists and physicists, and the students ranged from young postdoctorals to eminent physicists such as Leo Szilard who took the course in 1947. The importance of a quantitative and statistical approach to the new biology was stressed by the fact that a prerequisite for the first course (checked by an admission test!) was "facility in the processes of multiplication and division of large numbers; elements of calculus; properties of exponential functions."

The recruitment value to the phage field of these courses, probably first suggested by Luria (1), may be guessed from the fact that the total number of students over the years was well over 400, including many from abroad. Moreover, of some 130 students who attended the first ten courses, not less than 30 became recognized phage workers or bacterial geneticists so their initial interest must at least have been confirmed.

In addition to these courses, Max also organized a series of Phage Meetings, the first three of which were held at Nashville. The first meeting, in 1947, attracted only eight people, including Anderson, Doermann and Hershey. The fourth meeting, also organized by Max, was at Cold Spring Harbor in 1950 and thereafter the meetings continued there annually, without interruption, through 1981, attended by hundreds of participants.

In the early 1950s Max became interested in sensory perception and transduction and chose, particularly, to study the phototropic response of the large aerial sporangiophores

of the fungus *Phycomyces.* As in the case of phage, he became the leader of a *Phycomyces* Group, interested in various aspects of tropic behavior in this organism. From 1965 onwards Max organized the first of a series of eight *Phycomyces* Workshops, held at Cold Spring Harbor over the next twelve years. Each lasted about 2 months, they attracted, all told, more than 100 people, and Max led or participated in all of them.

The Cold Spring Harbor Laboratory therefore became a Mecca to which Max's followers in these two fields made their annual summer Hadj, not only to attend the more formal courses or workshops but also to continue their research in an exciting and stimulating environment. As James Watson, the present Director of the Laboratory, who became a PhD student of Luria in 1947, has reflected, "My approach to science as well as to people became indelibly fixed the following summer (1948) when we all came together at Cold Spring Harbor—the Delbrücks, the Lurias, Gunther Stent, Seymour Benzer and I—in an atmosphere that I can never remember as less than perfect. Now I realize that all the personality of Cold Spring Harbor, which I so loved then and still do, was given to it by Max" (3). It is therefore most fitting that a recently completed major extension of the Davenport Laboratory, the site of so much of Max's research as well as of the Phage and *Phycomyces* courses at Cold Spring Harbor, was dedicated as the Max Delbrück Laboratory in August 1981.

Return to Caltech

The war over, Max's preeminent role in the Phage Renaissance, and his novel and distinguished background as a theoretical physicist turned successful biologist, prompted offers, in 1946, of senior appointments at the Cold Spring Harbor Laboratory, the California Institute of Technology,

and the Universities of Illinois and Manchester, England. Vanderbilt University responded by promising him everything he wanted. He was especially interested in the Chair of Biophysics at Manchester, negotiated about May 1946 by P. M. S. Blackett who was then Professor of Physics, and Max visited there to discuss the appointment; he and his wife Manny were tempted to move to England because of the many attachments he had formed there in his early postgraduate years, while Manny had grown up in a British environment on the island of Cyprus. Max was also willing to listen to the Vanderbilt enticements. However, when the offer of a Chair of Biology at Caltech arrived on 11 December 1946 it proved irresistible, and was accepted on 27 December. This was the first faculty appointment in biology made by George W. Beadle who had recently succeeded T. H. Morgan as Chairman of the Biology Division.

If Cold Spring Harbor had become the Phage Mecca, visited by the converted for their intellectual refreshment, Max's laboratory at Caltech "now became the Phage Group's Vatican, where most of the disciples of what was later to be called the 'informational school' of molecular biology took their orders" (6). Recruitment followed fast from both the physical and biological sciences and "it is likely that the sense of excitement which often permeates a developing cluster must be generated by someone with Delbrück's charismatic force of personality" (5, p. 79). It is perhaps of interest that, during what Stent (17) has called the "Romantic Period" of molecular biology (up to 1953), about the same proportion of recruits to the phage field came from the physical sciences as from the biological sciences (5, p. 66). It is likely that an appreciable proportion of the former was motivated by Schrödinger's imaginative prediction about the nature of the gene in his book *What Is Life?*. Indeed, one of Max's colleagues at Caltech

at this time was Neville Symonds who came from postdoctoral studies on wave mechanics with Schrödinger, then working in Dublin as a former refugee from Nazi Germany. James Watson, on the other hand, whose interests and undergraduate background were in biology, admits that his main incentive was the "legendary figure" of Max evoked by Schrödinger's book.

Among the many phage devotees engaged in active research at Caltech during the early years of Max's leadership was Elie Wollman of the Pasteur Institute, Paris. André Lwoff, who was head of the Service de Physiologie Microbienne at the Pasteur Institute, had attended the 1946 Cold Spring Harbor Symposium and had there encountered Max and the Phage Group. He found the atmosphere stimulating and "swallowed everything with enthusiasm," but his interests at that time lay elsewhere; he did not attend the Phage Course nor start work on lysogeny until about 1949 (2, p. 88). Wollman was his first ambassador to Caltech, and thereafter many members of the American Phage Group worked for a time at the Pasteur Institute which became the European Vatican.

In 1949 the Delbrücks did not go to Cold Spring Harbor since Manny was expecting a child, so many of the Phage Group, including James Watson, came to Pasadena where "several times each week, there occurred seminars dominated by Delbrück's insistence that the results logically fit into some form of pretty hypothesis" (2, p. 239). Two new visitors to Caltech at this time were Ole Maaløe from Copenhagen University and Jean Weigle who was head of the Physics Institute in the University of Geneva; these two constituted a very small "Class of 49" that graduated under Max's supervision. (2, p. 265).

Weigle's account of his Caltech experiences, on his return to Geneva, decided to the electron microscopist, Ed-

ward Kellenberger, to apply his instrument to the study of phage (2, p. 116), while Weigle himself arranged with Max to spend his winters working at Caltech, and subsequently resigned his Geneva professorship for a wholetime Caltech research appointment. Maaløe also embarked on phage research in Copenhagen, and Watson worked with him there during the first year of his Fellowship in Europe in 1950, as well as with the Danish biochemist Herman Kalckar, who had attended the first Phage Course in 1945.

Thus, the gospel spread and its proselytes increased in number to discover that they had become members of an integrated, friendly and hospitable international family related by social as well as by intellectual bonds, with Max as their father figure.

DNA as Genetic Material

Max's early work on the one-step growth curve had shown that, following phage infection of bacterial cells, a latent period of about 20 minutes elapses before the cells begin to burst and liberate a hundred or more progeny particles. Mutation had also been revealed by Salvador Luria as the cause of variation in phage, as well as in bacteria as has already been recounted. Then Delbrück and W. T. Bailey (1946c) and A. D. Hershey independently (13) demonstrated genetic recombination when bacteria were doubly infected with phages that differed in two characters. This was the finding that led, about ten years later, to the ultimate genetic analysis of gene structure by Seymour Benzer (8). However, nothing whatsoever was known about the number or nature of the presumptive precursors inside the infected bacteria during the latent period. As Max remarked in a Harvey Lecture that he was invited to give in 1946, some 30 years after the first description of phage as a bacterial virus, "it should be our first aim to develop a

method of determining the number of virus particles which are present in a bacterial cell at any one moment. Here I, and those who have been associated with me in this work, have to make the first admission of failure" (1946b).

Such a method was first developed between 1949 and 1952 by A. H. Doermann (12) who disrupted cells at intervals after infection but failed to find any plaque-forming entities during about the first 12 minutes; thereafter infective intracellular particles began to appear and increased *linearly*. This "eclipse period" clearly showed that the phage changes its state immediately after infection, while the subsequent linear rather than exponential increase in phage numbers implied that this increase is not due to successive replications of its complete organism but is more compatible with an assembly of its component parts (see 2, p. 79).

At this stage it is interesting to note that Niels Bohr's influence and Schrödinger's prediction still retained a firm hold on Max's imagination. In an address entitled "A physicist looks at biology," delivered at the thousandth meeting of the Connecticut Academy of Arts and Sciences in 1949, he says,

> It may turn out that certain features of the living cell, including perhaps even replication, stand in a mutually exclusive relationship to the strict application of quantum mechanics, and that a new conceptual language has to be developed to embrace this situation. The limitation in the applicability of present day physics may then prove to be, not the dead end of our search, but the open door to the admission of fresh views of the matter. Just as we find features of the atom, its stability, for instance, which are not reducible to mechanics, we may find features of the living cell which are not reducible to atomic physics but whose appearance stands in a complementary relationship to those of atomic physics (1949b; also 2, p. 9).

In 1952 A. D. Hershey and M. Chase (14) published their famous experiment in which they infected cells with phage

in which the DNA and protein were differentially labelled with radioactive phosphorus and sulphur respectively; they found that the DNA entered the cells but that most of the protein, in the form of empty heads, remained outside. The eclipse was therefore the period during which the phage DNA was replicating and directing the synthesis of nascent phage protein. Thus, it turned out that the genetic material was DNA and that the genetic material alone entered the cell to initiate a new viral generation.

As early as 1944, Oswald Avery and his colleagues at the Rockefeller Institute, in New York, had published good biochemical evidence that the "transforming principle" of pneumococci, which transfers the hereditary ability to synthesize a polysaccharide characteristic of one type to bacteria of other types, is highly polymerized DNA. Why, then, did the Phage Group seemingly ignore this obvious clue to the chemical nature of the gene until a member of the group itself came to the same conclusion by a less rigorous experiment? In fact, both Max and Salvador Luria were very interested in Avery's work a considerable time before its publication, visited him at the Rockefeller Institute, and admired him as a person. In mid-1943 Avery wrote a long letter to his brother Roy, who was a microbiologist at Vanderbilt University and knew Max and showed him the letter which explained the results of Oswald's research and suggested, very cautiously, that DNA might be the genetic material (2, p. 180).

Although pneumococcal transformation was certainly seen as a very interesting phenomenon by Delbrück and Luria, there were then understandable reasons for failing to recognize its *genetic* importance. The phenomenon appeared to be uniquely restricted to polysaccharide production by a single bacterial species and seemed remote from the problems that beset phage workers. Moreover, at that time, bacterial

genetics did not exist, while DNA was generally regarded as a "stupid" molecule consisting simply of repeating tetrads of the same nucleotides which could hardly carry complex information; it was not until much later that contamination of transforming preparations with small amounts of protein, then favoured as the most likely genetic material, could be excluded.

However, the most cogent reason for failure to appreciate the importance of DNA in transformation was probably that it appeared as a biochemical problem, revealed by biochemical techniques. As Luria has said, "People like Delbrück and myself, not only were we not thinking biochemically, but we were somehow—and probably partly unconsciously—reacting negatively to biochemistry. . . . I don't think we attached great importance to whether the gene was protein or nucleic acid. The important thing for us was that the gene had the characteristics that it *had* to have" (4, p. 62).

But others had sensed the importance of DNA, confirmed by the Hershey–Chase experiment, and were working to elucidate its structure—an enterprise that culminated in the Watson–Crick double helix in 1953, a molecule that embodied all the genetic properties required by the gene (20). As soon as the model structure had been built and seemed right, James Watson revealed it first in a letter to Max (19), who was fascinated and thought it obviously right. Max then wrote to Bohr about the model, saying that he thought it equaled Rutherford's discovery of the nucleus of the atom (1).

Thus, as Gunther Stent has commented (18, p. 29), in one respect the Phage Group failed in its mission, for it did not discover the new laws of physics that Bohr and Schrödinger had prophesized. There turned out to be no paradox; only the hydrogen bond lay at the heart of the

mystery. The really important achievement of the Group during this romantic phase of the growth of molecular biology was "the introduction into microbial genetics of previously unknown standards of experimental design, deductive logic, and data evaluation. These procedures had led to final and definitive settlement of matters that had been under dispute for ten or more years" (17).

THE *PHYCOMYCES* PERIOD (1953–81)

Max was basically a theoretician who lived to search for neat models and hypotheses to explain complex phenomena. About 1950, after discovery of the phage eclipse phase but before the Hershey–Chase experiment, he became interested in sensory perception and its transduction into physiological activity—a phenomenon more relevant to the complex behaviour of higher creatures. He also thought that, by then, phage research was "in good hands." His first choice of a simple model organism was the purple bacterium, *Rhodospirillum*, which is not only photosynthetic but also phototactic, swimming towards a light source. Max was co-author of a general article on *Rhodospirillum* (1951b) in which the responses of this organism to light were compared with those of nerve fibers to electrical stimuli. However, after some early experiments he forsook this organism in favour of a simple fungus, *Phycomyces*.

Phycomyces has a non-septate mycelium which sprouts large aerial stalks called sporangiosphores, each crowned by a spherical sporangium containing many thousand spores. The attractiveness of this organism as a model for studying perception and response lay in the reactions of the rapidly growing sporangiophores to many stimuli. For example they grow towards the light (phototropism), against gravity (geotropism), into the wind (anemotropism), and away from nearby objects (avoidance response). On the other hand,

Phycomyces does not naturally form heterokaryons and produces multinucleate asexual spores, while the sexual cycle, involving two mating types that initially were far from isogenic, takes several months to yield recombinant progeny. Thus the organism lacks the ease and refinement of genetic analysis that made some other microbial systems, such as *Escherichia coli*, ideal tools in molecular biology.

Early studies of phototropism were initiated at Cold Spring Harbor in 1953 and the next year Max persuaded Werner Reichardt, then studying insect optomotor responses at Tübingen, to join him in his *Phycomyces* project. This partnership resulted in a classic paper (1956b) proposing a kinetic model of adaptation to light that proved influential for other sensory systems, although it has recently been shown to be adequate only for dark adaptation in the normal intensity range in the case of *Phycomyces* (E. Lipson, pers. comm.).

Thereafter a *Phycomyces* Group grew slowly, recruitment being mainly from physicists with no defectors from the Phage Group apart from Max himself. The Cold Spring Harbor workshops, each lasting about two months and beginning in 1964, attracted many participants from abroad who spread the gospel. Some regularly visited Cold Spring Harbor or Caltech for periods of collaborative discussions or research, especially from France, Germany, Japan, and Spain.

In 1969 the *Phycomyces* cause was further publicized by a comprehensive review of the whole field, to which 12 members of the group made specialized contributions. In his introduction Max stated, "This review, then, is addressed to those who aim to push sensory physiology to the limits of molecular biology. We believe that what can be learned from *Phycomyces* is relevant to this next phase of our quest for a mechanistic understanding of life." While agreeing that *Phycomyces* does not permit analysis of electrical sig-

nals, "which sensory physiologists have come to consider the *sine qua non* of their trade," nevertheless he believed that there is "much room for similarities in earlier stages of the transducer chain . . . and the receptor potentials of animal sensory cells, and it is to these as yet obscure stages that we think *Phycomyces* work can make a contribution of general relevance" (1969).

The adaptation range of *Phycomyces* to light is about ten orders of magnitude, equivalent to that of the human eye, and sensitivity is specific for blue light (1960). Max's main interest in recent years was the nature of the photoreceptor, the most likely candidate being β carotene or a flavin. With Katzir and Presti (1976a) he greatly extended the action spectrum and found absorption in the region of 600 nm which they interpreted as evidence for a flavin chromophore. Subsequently β carotene was excluded by the use of mutants in which its synthesis was undetectable (1977a, 1978b). Finally, in his last published paper, Max and his colleagues (1981) found that the substitution of an analogue of riboflavin (roseoflavin, with a distinctive absorption spectrum) in a riboflavin auxotroph produces an equivalent shift in the action spectrum. It thus seems likely that the sporangiophore blue light receptor of *Phycomyces* is a flavin and not a carotene, although the precise nature of the compound remains unknown (see 15).

In the years that have elapsed since the 1969 review, much interesting work and some important technical advances have been made, especially in the field of behavioural genetics. For example, the introduction of a microsurgical technique for making heterokaryons and the development of isogenic mating types have revolutionized genetic analysis. A large number of behavioural mutants have now been isolated, involving photoresponses to sporangiophore development and carotene synthesis as well as various tro-

pisms. In addition, other mutants affecting the pathway of carotene biosynthesis have been obtained. Classification of these mutants according to their functional and sequential relationships is clarifying the organization of their underlying sensory pathways (review 15).

Although it is true that no major breakthrough has been made in understanding the basic mechanism of sensory transduction, this is also the case for other systems. It has been suggested that progress might have been quicker if more effort had been directed toward developing the basic genetics and biochemistry of *Phycomyces* during the early period. Only the physiological aspects were then energetically pursued, resulting in a lot of models unsupported by strong experimental evidence (A.P.E.).

Although Max remained dedicated to *Phycomyces* from 1953 onwards, he did not lose touch with phage research. Thus, with N. Visconti he developed a mathematical model of phage recombination based on multiple rounds of mating during the eclipse period (1953) while, a little later, he became interested in theoretical problems of DNA replication (1945b, 1957) and the genetic code (1958b).

The Cologne Interlude (1961–63)

After the war Max returned to Germany on several occasions, first in 1947, and then in 1954 when he visited Göttingen for 3 months. In 1956 he was invited to spend 3 months at Cologne by Josef Straub, who was Professor of Botany at the University and wanted Max to bring molecular genetics to his new institute which was among the first being built at that time. Max gave a phage course in the unfinished new building, still without electric light or concrete floors, "which was quite a tour de force" (1). It was during this course, at which Peter Starlinger (now Director of the Institute) came from Hamburg to give a seminar, that the

idea took root of a Genetics Institute embracing several independent, integrated groups headed by professors, but having many facilities in common and an emphasis on research. This was a very novel concept for Germany and it was hoped that Max would agree to become the first director so that his reputation could be used in negotiations with the Government; but Max agreed for 2 years only, on leave of absence from Caltech, in the unlikely event of the project materializing.

A first step was the appointment of Carsten Bresch to a Chair of Microbiology in the Botany building, where he was joined by Rudi Haussmann, Peter Starlinger, Thomas Trautner, and A. H. Doermann who spent a sabbatical 1957 with them (P.S.). Then in 1959, thanks to the extraordinary negotiating ability of Josef Straub, the Institute was finally approved. During the developmental stages, Max visited Cologne about once a year to discuss plans for the future, and succeeded in obtaining funds from a semi-private organization for two additional senior staff appointments which the university could not afford.

The Institute of Genetics building was eventually completed, and the staff moved during the summer of 1961. The Institute was formally dedicated in June 1962, with Niels Bohr as the principal speaker. His lecture, entitled "Light and life—revisited," commented on the original one of 1933, which had been the starting point of Max's interest in biology. It was to be Bohr's last formal lecture. He died before completing preparation of the manuscript of this lecture for publication (but see Delbrück 1976; also 10).

Max organized four groups of workers, under Carsten Bresch, Walter Harm (radiobiology), Peter Starlinger and Hans Zachau. In addition, he formed a group of his own which, surprisingly, he devoted to the study of the photochemical effects of ultraviolet light on DNA which had in-

terested him since the then recent discovery of thymine dimers (e.g., 1962b; 1963b).

Max also found time to talk to and encourage younger workers, and he established internal seminars which the whole Institute was supposed to attend in order to foster interactions. In addition, phage courses on the Cold Spring Harbor model were run every year from 1962 onwards, and in 1963, at Max's persuasion, a course on bacterial genetics was added (P.S.).

When Max left in 1963 he agreed to maintain connections with the Institute and was appointed as Honorary Professor. For some years thereafter he returned to Cologne every year or so to give a series of lectures, or just a seminar, often on a topic outside the normal curriculum. In Starlinger's opinion, Max's Cologne period was beneficial to German biology as a whole, not only on account of the courses he instituted, but also because of his extensive travelling and lecturing.

Later he was persuaded to serve as an adviser in natural science on the Founding Committee of the new University of Constance. "This led to a natural sciences faculty that was essentially all molecular biology—even the chemistry and physical chemistry were all molecular biology" (1). An agreement was reached with the university that he would spend one semester there in every six, but he did this only once, in the summer of 1969, when he indulged his more physical and mathematical interests (e.g., 2-D diffusion) with friends there. That was his and Manny's last long visit to Germany.

PERSONALITY

How can I begin to describe what Max was like to those who did not know him, for he was all things to those who did? His profound intelligence and scholarship in so many

fields of science, philosophy and the arts, all of which he regarded as a cultural unity; his blend of critical and quiet-spoken aloofness with outgoing gregariousness, affection, and sense of fun; his basic seriousness and childish love of practical joking; all could be seen as the essence of paradox, or as the embodiment of "natural man." This, perhaps, has been best expressed by a close colleague of Max (D.R.S.) who "always thought of Max as a human archetype." Perhaps the best way to convey an impression of Max's individuality is through a kaleodoscope of reminiscences and impressions by various friends who knew him well.

I remember vividly the discussions that we had and also the discussion among the circle of friends about physics, philosophy and human problems. Max was able to attract the best and most interesting people because of his wonderful personality and his direct approach to questions of interest. Many people know him as rather acid and critical, and sometimes even arrogant. It is true that he did not well tolerate half-truths and superficial remarks, but he was a warm friend to those whom he valued, and he was always ready to help, to discuss the problems and, last but not least, to have fun with his friends (V.F.W.).

He abhorred the petty and in searching for the deepest of theories insisted that we work together in a collective generous fashion. The selfish and the avaricious were not tolerated, and those unfortunate souls who could only so survive, were not for Max. . . . He also had no use for stuffiness or protocol and was never Professor or Dr. Delbrück but Max to all who would learn with him (J.D.W.; 3).

He was a compassionate man, very honest, with a slow but strong and deep intelligence (Germany style); he was half philosopher, half physicist, with a scale of values very different to the common scientific man. He enjoyed life every minute. He loved to talk with people and it is remarkable how he concentrated his mind to listen to them (A.P.E.).

His playfulness translated quite literally into plays, the marionette shows he put on with his children, in which in a marvelous conceit, he often took the role of Uncle Max, the fusty professor with a thick German accent.

Max was Max and sometimes he played Max. He also proposed to play Samuel Beckett, threatening to give the latter's Nobel acceptance speech for him when he failed to go to Stockholm (in 1969). He particularly admired the work of Beckett because, almost as a scientist, Beckett had reduced the complexities of human intercourse to their elements, a series of games turning in an eternal round (D.R.S.).

. . . Delbrück's had been a kind of Gandhi of biology who, without possessing any temporal power at all, was an ever-present and sometimes irksome spiritual force. "What will Max think of it?" had become the central question of the molecular biology psyche (G.S.S.).

Among the most memorable features of life with the Delbrück group at Caltech was the extraordinary and informal hospitality of Max and Manny in their home in Pasadena which was "open house" to all and sundry; and the famous weekend camping trips to the desert, organized by Manny, that might include undergraduates, graduates, post-docs, staff, visitors, children and dogs, with long treks up and down the hills and canyons, on which Max might unexpectedly block the path by stopping abruptly to ponder a sudden thought. After returning to camp and a welcome siesta, Manny would prepare dinner over the camp fire. "Evening brought a big fire and wild stories until each wandered into the dark to find his own bag and pile of clothes under the sky freckled with stars. Yes *stars*! One would occasionally wake up to see a naked Max balancing his binoculars against the car. He was charting the movement of the planets and rediscovering for himself these movements as the ancients had done it" (N.D.). In recent years Max continued to enjoy desert trips and often he and Manny would take small groups of friends for mid-week picnic walks and talks over rough country closer to Pasadena.

Another more disciplinary aspect of Max's style is recalled by Seymour Benzer.

The urge to do experiments was always so strong that we could not get ourselves to sit down and write up the results. Delbrück had a solution for this. He assembled all who had papers to write and whisked us off to Caltech's Marine Biology Station at Corona del Mar. There, we were locked up for three days and ordered to write. Delbrück's wife, Manny, typed as rapidly as we could spew the stuff out; we mercilessly criticized each other's drafts, and in three days everyone had completed a paper (2, pp. 157, 340).

Sense of Humour

Max's wit and humour were very much a part of his image because they accentuated the depth and seriousness of his personality in such a striking way. His wit was light and amusing, as when he told Jean Weigle that he supposed the *Festschrift* in honor of his (Max's) 60th birthday would be an opportunity for everyone to publish papers that had been rejected repeatedly by many journals. Again, he propounded his "Principle of limited sloppiness" to account for the emergence of important ideas from experiments that had not been rigorously controlled.

Another example of his wit, as well as of the playfulness mentioned above, is his introduction to the Commencement Address he delivered at Caltech in 1978, entitled "The arrow of time" (11). It appeared that a committee had suggested Max as speaker, while the students had again suggested the comedian, Woody Allen. "So," said Max, "what happened? Well, it's up to you to decide. Is it Max Delbrück as advertised, talking to you, or is it Woody Allen, impersonating a Senior Academic Citizen, scurrilously named Max Delbrück, or is it Max Delbrück, scurrilously pretending to be Woody Allen impersonating Max Delbrück? Having been trained in critical thinking for so long at Caltech I am sure you will enjoy pondering these alternatives while I, whoever I may be, go on with my talk"; and on he went to discuss very seriously the paradoxes of the nature

of subjective and objective time, and of truth. Incidentally, I see in the margin of a copy of this address that he sent me the annotation, "Letter follows—but when?"!

Max's more farcical sense of comedy must be mentioned since it is an aspect of his personality that his friends remember so well, and which proved rather infectious within the Phage Group. For example, a British physicist (C.F.) who knew him in Berlin in 1937 remembers a summer party at his home to which "he invited half the guests in evening dress and the other half in casual tennis clothes, and he himself wore his grandfather's tail coat over old flannel bags."

In much the same vein, a visitor to Caltech in 1953 (E.S.A.) was invited to accompany the Delbrücks to a perfectly sober end of term students' play. To his astonishment, Max insisted on dressing up as a pregnant woman and Manny as "her" English husband, complete with moustache, bowler hat and furled umbrella, while he (E.S.A.) went as a friend attired in weird clothing. They arrived late at the play and "you can imagine the sensation we produced as we marched solemnly down the aisle to our seats near the front." Max and his party left before the end of the play, and it then transpired that the cast and many students and friends had been invited to the Delbrück home after the performance. Max now insisted that he and his guest exchange roles on the grounds that the prank would not otherwise be complete—a dénouement "which resulted in the utmost confusion when the guests arrived."

When Max was at Cologne he introduced a lifestyle that was quite atypical for Germany, such as organizing a treasure hunt through the whole of Lindenthal, while at parties in the Institute "there would be rather skillful cartoons exhibited, and sketches would be performed which would make fun of the Institute and mainly of the senior people" (P.S.). Of course, Max was sometimes "hoist with his own

petard." For instance, it was his habit at Cologne to attend all the lectures of a course, reading a newspaper during the morning session, and then giving the last lecture himself. On one such occasion he was confronted, at *his* lecture, by the whole class who "pretended to be busy with their newspapers too. Max was a little startled at first, but then took it with good humor" (P.S.).

Finally, to show how intimidating Max might at first appear to those who didn't know him well, it was not uncommon for him, with a rather serious expression, to say to a lecturer after his performance, "Well, that was the worst seminar I have ever heard!"; but I should conclude this theme by saying that at least one victim of this comment of Max, George Streisinger, also recorded "the very great love and admiration that so many of us feel towards him" (2, p. 335).

The Intellectual Man

In the winter of 1972 Max gave an extensive course of 20 lectures at Caltech on "Evolutionary epistemology." He later condensed these into a long but elegant essay entitled "Mind from matter??" presented as a single lecture to the XIIIth Nobel Conference in 1977 (1978d). The essay ranges from cosmology and the beginning of life, through the evolution of prokaryotes and perception, higher organisms and behaviour, the nervous system, consciousness, language and culture, to cognitive ability. He then goes on to ask, if mind evolved and was selected merely for its survival value, "to let us get along in the cave, how can it that (it) permit(s) us to obtain deep insights into cosmology, elementary particles, molecular genetics, number theory? To this question I have no answer. . . . The feeling of absurdity that attaches to the notion "Mind from Matter" is perhaps of a similar nature to the feeling of absurdity we have learned

to cope with when we permit relativity to reorganize time and space and quantum theory to reconcile waves and corpuscles. If so, then there may yet be hope for developing a formal approach permitting a Grand Synthesis." The essay begins with a brief recapitulation of Schrödinger's book, *What Is Life?*, and outlines Bohr's subtle complementarity argument. Thus Max's thinking continued to be swayed by Bohr's ideas, but in a new dimension, after 45 years.

However, my main object in mentioning this essay, and the series of lectures that begat it, is to emphasize the cosmic scope of Max's conceptions, and the breadth and quality of his educational influence at Caltech. Max taught regularly at Caltech and his "method of learning was to teach, and every year . . . he would assign himself the task of teaching a course in some new subject that *he* wanted to learn. This ranged all the way from statistical mechanics to epistemology. So Max became an expert in every one of those subjects. As recently as a year and a half ago, long after he had been officially retired, he volunteered to teach freshman physics here at Caltech as a sort of refresher course for himself" (S.B. 3). In fact he never lost his interest or skill in theoretical physics and mathematics and, as late as 1980, published a paper on Bose–Einstein statistics (1980a). Papers on *Phycomyces* phototropism continued to appear up to the year of his death.

However, his interest in formulations of objective reality was by no means limited to the modern era, but went back to Aristotle for whose biological observations and speculations he had great respect although his physics, as might be expected, rated "pretty much of a catastrophe." In his article, "How Aristotle discovered DNA" (1976c; see also 1971), Max explains, with many quotations, Aristotle's hypothesis that the male semen carries the *form principle* or plan of inheritance which does not become part of the

embryo, unlike Hippocrates's theory that the semen consists of extracts or miniatures of each part of the body as in the later homunculus model. Indeed, two of Aristotle's arguments from observation, that the semen may determine either male or female, and that inheritance of skin colour can skip a generation, could well have served as a basis for Mendel's laws! (W.H.). Max goes on to recount the history of Aristotle's manuscripts (initially published in the *Scientific Athenian*!), and the final, accidental appropriation by theologians "of the most secondary and misguided aspects of Aristotle's speculations. It is due to this bizarre twist that we are encumbered today with a total barrier of understanding between the scientists and the theologians, from St. Thomas Aquinas to today."

David Smith, Associate Professor of Literature at Caltech, writes of Max, "His interest in the humanities was profound, of long duration, and increasing intensity. And it was a matter of day to day practical observance, as most things profound are. He often attended humanities seminars. He even sponsored one. . . . He was the most active supporter of the art gallery on the campus." Indeed the Berlin artist, Jeanne Mammen, was supported and encouraged for decades by Max but received recognition only after his death.

Poetry was of particular interest to Max and he was invited, in 1980, to lecture at the Poetry Center in New York, in the wake of such predecessors as T. S. Eliot and Dylan Thomas. He intended to talk about Rilke who interested him as the most intuitive of major German poets. Unfortunately, this fell through because of illness, but he had hopes for 1981 and had completed nine pages of his lecture at the time of his death, in which "he pursues Rilke's imagery, its sources, the shock value of image and syntax. He compares and criticizes translations, translates himself. He comments on the use of symbol, vocabulary,

rhythm. He was intensely and poetically interested in words" (D.R.S.).

Max's musical tastes were classical, with a special liking for J. S. Bach. He played the piano poorly but with some enthusiasm, and taught himself the alto recorder well enough to play chamber music in home ensembles.

LAST DAYS

When Max reached the normal age of retirement in 1977, the Caltech trustees appointed him to the special position of Board of Trustees Professor of Biology, Emeritus, so that he could continue the research of his *Phycomyces* Group at the Institute. Early in 1978 he learnt that he was suffering from multiple myeloma, a cancer of the plasma cells of the bone marrow. This responded well to chemotherapy, apart from occasional remissions and the need for blood transfusions, so that he was able to travel to Paris with his daughter Nicola in the spring of 1979 to be inducted as a Foreign Member of the French Académie des Sciences.

He retained the interest of a scientist towards his disease from its beginning, never complained, and, from first to last, retained the upper hand. A few months before his death he suffered a mild stroke which impaired his vision on one side; he found this more interesting than disturbing, and smilingly said, "The students need me as a guinea pig; they are setting up some tests they cannot do with the monkeys" (B.C.).

When Max first learnt about his illness he started a diary which he called "Heimreise" ("Journey Home") to record his thoughts about its progress. Here are two entries:

"Wohin gehen wir denn?" ("Where are we going?")
"Immer nach Hause" ("Always toward home")

This quotation was written on 24 September 1978, and his

thoughts on this theme were: "The journey of life which seems to be going outward, in the end turns out to have been going inward most of the time." On 5 March 1979 he wrote, "Im leichten Wellenschlag der Wochen treib ich dahin. Ein steuerloses Blatt bald zu verschwinden." ("I drift with the gentle undulation of the weeks. A rudderless leaf soon to disappear.")

During the last few weeks of his life, Max announced one day that he had decided to live for two more years in order to complete his autobiography which he had recently started to write. Only 3 days before his death he began to dictate the chapter "Light and life" (B.C.).

I WISH TO RECORD my most grateful thanks to Max's wife, Manny Delbrück, for her invaluable help in compiling this Memoir and commenting on the draft manuscript, and also to their daughter Nicola (N.D.) for her impressions of family life. Dr. Patricia Burke kindly provided me with a full bibliography, compiled with Manny's assistance, and Professor L. Hood provided an up-to-date list of Max's honours and other data. I am also indebted to many people who offered me impressions and reminiscences of Max. Personal and scientific recollections of his early career in theoretical physics were sent to me by Professor Sir Charles Frank, O.B.E., F.R.S. (C.F.) who also put me in touch with the University of Bristol, Dr. G. Herzberg, F.R.S., Professor N. Thompson (N.T.), and Professor V. F. Weisskopf (V.F.W.). Professor A. P. Eslava (A.P.E.) and Dr. E. D. Lipson provided assessments of the work of the *Phycomyces* Group, and Professor P. Starlinger (P.S.) enlightened me on the conception and birth of the Cologne Institute. Dr. P. M. Gresshoff, Professor G. S. Stent, and Professor M. J. D. White, F.R.S. kindly suggested appropriate amendments to the draft manuscript. Finally, I must also thank the following for permitting me to quote from their personal communications, contributions to Max's Memorial service, and other unpublished sources: Professor E. S. Anderson, F.R.S. (E.S.A.), Professor S. Benzer (S.B.), Fraulein Beate Carrière (B.C.) who recorded the last few weeks of Max's life (translated for me from the

German by Dr. P. M. Gresshoff), Dr. D. R. Smith (D.R.S.), Professor G. S. Stent (G.S.S.), and Dr. J. D. Watson (J.D.W.).

(The initials in brackets indicate the sources of quotations in the text.)

FAMILY

Married: 2 August 1941, Pasadena, California, to Mary Adeline Bruce (born 1917 in Butte, Montana, U.S.A.), daughter of James Latimer Bruce, mining engineer, and Leah Hills Bruce.

Children: son, Jonathan, born 1947 in Nashville, Tennessee;
daughter, Nicola, born 1949 in Pasadena, California;
son, Tobias, born 1960 in Pasadena, California;
daughter, Ludina, born 1962 in Cologne, W. Germany.

HONORS

Election to

U.S. National Academy of Sciences—1949
American Academy of Arts and Sciences—1959
Royal Danish Academy—1960
Deutsche Akademie der Naturforscher Leopoldina—1963
Royal Society of London, Foreign Member—1967
Académie des Sciences, Paris, Associé Étranger—1979

Honorary Degrees

Copenhagen University—1965: Doctor of Philosophy
University of Chicago—1967: Doctor of Science
Heidelberg University—1968
Harvard University—1971: Doctor of Science
Gustavus Adolphus College, St. Peter, Minnesota,U.S.A.—1977: Doctor of Science
University of Southern California—1981: Doctor of Science
Göttingen University—1981: Doctor of Philosophy (to commemorate 50th anniversary of first degree)

Awards

Kimber Medal for Genetics (U.S. Academy of Science)—1964
Gregor Mendel Medal (Deutsche Akademie der Naturforscher-Leopoldina)—1967
Gross-Horwitz Prize (Columbia University)—1969
Nobel Prize for Physiology or Medicine—1969

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