HENRY G. KUNKEL

1916-1983

An Appreciation of the Man
and His Scientific Contributions

&

A Bibliography of
His Research
Papers

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DURING his long tenure as an Editor of *The Journal of Experimental Medicine*, Henry Kunkel's scientific interests and brilliant research accomplishments were major factors in shaping the development of the Journal. It seemed appropriate, therefore, to publish this tribute to our colleague at the time of the Scientific Symposium on Modern Immunology sponsored in his honor by The Rockefeller University on May 8, 1985.

We originally considered reprinting a selection of his most seminal papers. However, this proved infeasible because of their number and the widely differing opinions as to which to select. Instead, we have chosen to reflect the scope of his work by publishing a bibliography of his research papers, including essentially all of the primary publications of his experimental work but omitting abstracts, reviews, book chapters, lectures, and the like. A listing of the latter items will be available in the Rockefeller University Archives.

The bibliography is prefaced by tributes from three of Dr. Kunkel's colleagues: Alexander G. Bearn, Frank J. Dixon, and Baruj Benacerraf, who were among his most treasured professional associates and personal friends. Although it has not been possible to divide Dr. Kunkel's career into separate, well-defined periods, Dr. Bearn has focused primarily on the early years, including the work on liver disease and antibody globulins; Dr. Dixon, on the middle years, encompassing the work on antigen-antibody complexes, lupus erythematosus, and rheumatoid arthritis; and Dr. Benacerraf, on the work related to the structure and genetic control of immunoglobulins as well as the later studies on idiotype and cellular immunology. Drs. Bearn, Dixon, and Benacerraf have long been associated with the Journal, having served as Advisory Editors since this category was first established.

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The Editors

I.

In 1951, I was invited by Henry Kunkel to work at the Rockefeller Institute for Medical Research. I remained at the Institute for fifteen years, seven of which were spent in the Kunkel laboratory. In this way, I was privileged to witness the early flowering and rapid development of a remarkable scientific career.

When I arrived at the Institute, Henry Kunkel was thirty-four years old and had already published twenty-six scientific papers, two of which had survived the critical editorial eye of Peyton Rous and had been published in *The Journal of Experimental Medicine.* In 1960, Peyton Rous invited Kunkel to join the editorial board, on which he served with great distinction and undiminished pleasure until his death at the age of 67.

Henry Kunkel's interest in the biological sciences began at home. His father, the distinguished plant pathologist Louis Otto Kunkel, had been invited in 1931 to set up a new department of plant pathology at the Rockefeller Institute. Louis Kunkel was still there fourteen years later when Henry joined the Rockefeller, where he was to spend his entire research career. For more than half a century, without interruption, the Kunkel name was on the roster of the Institute's distinguished faculty.

When Henry Kunkel arrived at Rockefeller, after completing his residency at Bellevue Hospital, he joined the laboratory of Charles L. Hoagland, who was investigating epidemic infectious hepatitis for the Navy. Kunkel's early studies were largely clinical, but the biochemical abnormalities, particularly those affecting serum gamma globulin, aroused his special interest and attention.

Two years after coming to the Institute, Kunkel, wishing to follow the chemical as well as the clinical course of liver disease, devised a very sensitive quantitative turbidimetric flocculation test using zinc sulfate, which received wide acceptance in clinical practice. He had also published his first paper in *The Journal of Experimental Medicine,* showing that plasma esterase was synthesized by the liver. He went on to show that, in the hypoproteinemia associated with liver disease, the liver was unable to synthesize plasma esterase, whereas, in hypoproteinemia characteristic of the nephrotic syndrome, the liver's capacity to synthesize esterase was increased.

One year after Kunkel came to Rockefeller, Hoagland died, at a tragically young age; shortly thereafter, Kunkel was appointed head of the laboratory. His next several years, despite the absence of a laboratory mentor, were filled with clinical and scientific achievement. He characterized two new syndromes in liver disease in sufficient clinical and biochemical detail that they remain recognizable as distinct entities to this day. The first was a form of cirrhosis of the liver that was predominantly seen in young females. Hormonal disturbances were occa-

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sionally seen, and a marked hypergammaglobulinemia was a frequent and arresting feature. Many of the patients had active arthritis, and their blood yielded a positive lupus erythematosus reaction. These patients were sometimes affectionately called "Kunkel's girls," to Kunkel's evident discomfiture.

The second syndrome, described in collaboration with Edward H. Ahrens, Jr., was a form of cirrhosis with marked hypercholesterolemia and xanthomatosis, and was designated primary biliary cirrhosis. Both syndromes remain of current interest. The exact nature of the hormonal disturbances in chronic active hepatitis and lupus erythematosus are still being investigated in the Kunkel laboratory, with the use of modern methods.

In 1950, Henry Kunkel, now thirty-three years old, spent a pivotally important year abroad in the laboratory of the Nobel laureate, Arne Tiselius, in Uppsala. That year was enormously valuable for Kunkel, not only for what he accomplished but for the direction it gave to his career in science. When he sailed for Sweden, he knew that he wanted to understand pathogenetic mechanisms of human disease at a deeper and more intellectually satisfying level. While in Uppsala, Kunkel learned the technique of free solution electrophoresis and, with Tiselius, wrote a paper in *The Journal of General Physiology* discussing the physical chemistry underlying paper electrophoresis. These studies impressed Vincent du Vigneaud, Professor of Biochemistry at Cornell University Medical College, who was later to win the Nobel Prize in Chemistry. On Kunkel's return, he and du Vigneaud described the electrophoretic properties of the polypeptide oxytocin, including a determination of its isoelectric point.

Kunkel's efforts at characterizing the properties of proteins separated electrophoretically were frustrated by the inadequate amount of protein that could be eluted by paper electrophoresis. To overcome this difficulty, Kunkel investigated a variety of supporting media that might enable adequate amounts of protein to be eluted from serum separated electrophoretically. He found that commercial starch, meticulously washed, allowed separation of large volumes of serum into sharply distinct electrophoretic components. Scores of investigators came to the Kunkel lab to learn the technique. Like so many that Kunkel devised, it was simple and elegant and led to discoveries in fields of science far removed from his own.

Kunkel had always been interested in immunology. Even before leaving for Uppsala, he had published a paper in the *Journal of Biological Chemistry* on the immunologic determination of human albumin in biological fluids. Classical immunologists were reluctant to abandon the time-honored method of measuring precipitated antibody, using the micro-Kjeldahl technique, but Kunkel was impatient with its tedium and was eager to find simpler techniques to help him investigate the immunologic aspects of disease. He soon became a master at extracting critical information from the simple Ouchterlony plate; because of his meticulous attention to experimental detail, he often made discoveries that others would miss.

The increase in serum protein that Kunkel had observed in some patients with cirrhosis of the liver was also found in patients with multiple myeloma. In the latter, however, such proteins, known as myeloma proteins, were thought to be abnormal products derived from the malignant cell. In a series of experiments of outstanding simplicity, Kunkel made the far-reaching discovery that these

proteins, so greatly elevated in the serum of patients with multiple myeloma, were related to normal gamma globulin. This discovery led to studies by his student, Gerald M. Edelman, which established the structure of human gamma globulin and subsequently earned Edelman the Nobel prize.

By the late 1950s, Henry Kunkel was widely recognized as a brilliant clinical investigator, and a steadily increasing stream of young investigators sought opportunities to work with him. Kunkel's interests widened, and he turned to other clinical problems that posed immunologic challenges, including lupus erythematosus and rheumatoid arthritis. Because of his belief that clinical observation often leads to pathogenetic clues that can be followed up in the laboratory, patients with lupus erythematosus and rheumatoid arthritis were admitted to the hospital of the Rockefeller Institute.

Kunkel and his colleagues demonstrated the presence of autoimmune complexes in rheumatoid arthritis. They further showed that rheumatoid factor was a 19 S IgM-type autoantibody to 7 S IgG, and occurred in the circulation as a soluble complex with IgG. He also described the presence of immune complexes of DNA, and other cellular components, in the circulation of patients with systemic lupus erythematosus. The severity of the disease could be related to the presence of circulating immune complexes. These complexes were deposited in the glomerular basement membrane where they activated complement and led to lupus nephritis.

Even as his immunologic interests deepened, Kunkel made a discovery of great importance in a field removed from the mainstream of clinical immunology. Using starch-block electrophoresis, Kunkel observed a previously unrecognized component of normal human hemoglobin, which he named hemoglobin A_2. Turning to hemoglobin obtained from individuals with genetic diseases, he found that, in patients with thalassemia minor, the Hb A_2 component was strikingly increased. The test proved so reliable that the measurement of Hb A_2 level not only became the standard diagnostic procedure throughout the world for identifying carriers of the thalassemia gene, but also fueled the growing interest in the field of abnormal hemoglobins.

Despite highly productive sallies into other fields, the focus of the Kunkel laboratory was becoming apparent—to unravel the mysteries of the immune system through the study of human disease. In this scientific quest, Kunkel became the renowned leader.

I would be remiss in closing this brief account of the early work of Henry Kunkel without making some personal observations. Those fortunate enough to be in the Kunkel laboratory in those early days were quickly infected by his zest for research and new discovery. We learned that conducting experiments was a form of thinking for which no library could substitute, while we profited from his example and generosity. Beyond this, we recognized that, for Henry Kunkel, a spectacular career of high scientific achievement lay ahead.

II.

In his first decade of research, Henry Kunkel devoted much time to the development of the tools of protein chemistry and immunology that were to serve him so well throughout his career. In spite of his emphasis on the laboratory, however, he remained very much a physician, and the origins of his research usually derived from clinical observations. His first research interest, liver disease, led him to study the associated changes in serum proteins, particularly gamma globulin. Gamma globulins, poorly understood at the time, became a continuing interest; today they are genetically, chemically, and functionally among the most completely characterized of proteins, in no small part the result of his efforts. His interest in liver disease led him to two other diseases: systemic lupus erythematosus and rheumatoid arthritis, which became central themes in his investigative career and marked the beginning of the second phase in his research. During the study of these two diseases, one of the major characteristics of his research became evident, i.e., the emphasis on the pathogenesis of disease, particularly immunologic disease. Throughout the course of his chemical and/or genetic analyses of immunologic molecules, he was always concerned with how these molecules might participate in the pathogenesis of one or another disease.

Henry was preeminent as a clinical investigator, and one of his greatest strengths was the ability to recognize those clinical entities that would provide the most fruitful insights and leads when analyzed by available technology. His recognition in the late 1950s that 19 S antibodies reacted with 7 S gamma globulin in the sera of patients with rheumatoid arthritis, provided just such a lead. These rheumatoid factors served many purposes: they were model 19 S antibodies; they served as convincing examples of autoantibodies at a time when the existence of immunologic autoreactivity was far from established; and, when combined with their 7 S gamma globulin "antigen," they were examples of immune complexes in serum or synovial fluid that were apparently related to the pathogenesis of rheumatoid arthritis.

Systemic lupus erythematosus proved to be equally profitable as a source of new leads. Henry discovered and characterized some of the many autoantibodies in lupus. Of particular interest were the antibodies reactive with nuclear antigens, especially DNA, which seemed to correlate with the activity of the disease and were responsible for lupus erythematosus cell phenomenon. His attempts to link these autoantibodies to the pathogenesis of the disease then led to the identification of immune complexes in the circulation and in deposits at the sites of tissue injury. These observations provided some of the strongest evidence for the pathogenic role of immune complexes in human disease and established systemic lupus erythematosus as the prototypic immune complex disease.

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Today, Henry's work on rheumatoid arthritis and systemic lupus erythematosus, as described in his papers beginning in the late 1950s, appears to be a perfectly orderly and highly productive dissection of two immunologic diseases, using the new tools of protein chemistry and immunology. However, when considered in the context of the immunologic dogma of the day, these studies were revolutionary. Rheumatoid factor was considered by many to be a factor of undetermined character until Henry's unequivocal demonstration of its antibody nature. Also, there was still intense debate about the existence as well as importance of autoantibodies until he, along with a few others, demonstrated their abundance in clinical cases of systemic lupus erythematosus. Further, there was no good explanation for the possible pathogenicity of such autoantibodies in systemic lupus erythematosus until he proposed an immune complex mechanism similar to that which had been demonstrated in experimental serum sickness. This was indeed pioneering work that contributed to our present concepts of immunopathology. In addition, it provided important examples of the value of laboratory observations in the study of clinical material and helped set the standards for the fledgling field of clinical research.

There is a dimension of Henry's contributions to medical science that is not apparent from his bibliography. This was his considerable editorial influence on immunologic literature, a literature that was destined to increase more than twenty-fold during his career. As an editor of *The Journal of Experimental Medicine*, he was instrumental in increasing that Journal's immunologic orientation, in keeping with the explosive growth of the field. In the eyes of many, *The Journal of Experimental Medicine* became the most prestigious forum for immunologic studies. Also, as a long-time coeditor of the widely read series, *Advances in Immunology*, he had a strong positive influence through the wise choice of authors and of promising subjects for review. In addition, he served on the editorial boards of numerous other immunologic and clinical journals, where his high standards were an important influence. We can truly say that the story of the development of immunology, as recorded in its numerous publications, is much the better for Henry's editorial influence.

III.

THE tragic death of Henry G. Kunkel at the height of his productive career was deeply felt by the international communities of immunologists and clinical investigators, of which he was an undisputed leader. He will be sorely missed by his many devoted students and associates, and by his admiring colleagues and friends.

Henry Kunkel was one of the giants of an era that saw the explosion of immunology as a molecular science and the development of clinical investigation as a discipline. He was a rare combination of perceptive, imaginative scientist and accomplished and subtle clinician, who brought the most rigorous molecular techniques to bear on the analysis of highly complex pathological processes. In so doing, he played a key role in shaping these disciplines at a critical time in their evolution. He had the uncanny ability to use unique clinical material to make fundamental, broadly applicable discoveries. He was also an incomparable teacher, able to inspire in his students a lasting dedication to the goals and ethical and scientific standards that governed his own professional life.

I feel deeply privileged for the opportunity to express my feelings of admiration and respect as well as my personal grief at his untimely loss. In this brief tribute, I will recall some of the many landmark contributions that Henry Kunkel made to immunology, and the profound impact that he had, as a teacher, on his numerous disciples.

Henry Kunkel began his research career at a time when immunology was a phenomenological science. Nothing was known of the structure of antibodies, their classes, or the immunoglobulin genes. Furthermore, the elucidation of the molecular structure of antibodies was made extremely complex by their heterogeneity, which rendered analytical studies of homogeneous antibody molecules impossible. Faced with this difficulty, Kunkel wisely decided that myeloma proteins are monoclonal molecules representative of the heterogeneous population of gamma globulins (Kunkel et al., 1951). This approach, which presented immunochemists and immunogeneticists with homogeneous molecules to analyze and compare, made possible the dramatic advances in his and other's laboratories that identified the antibody classes, immunoglobulin chains, immunoglobulin genes, and the variable and constant regions of immunoglobulin chains. It was while working as a student in Kunkel's laboratory that Gerald Edelman (1) demonstrated that reduced and alkylated gamma globulins and myeloma proteins could be dissociated into their component chains. Moreover, in 1951, Kunkel's realization (Kunkel et al., 1951) that myeloma proteins, the monoclonal products of malignant plasma cells, were the equivalent of normal antibodies produced by normal plasma cells, led to the demonstration that Burnet's clonal theory of

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antibody production was correct, and eventually provided immunologists with the tools and approaches to develop monoclonal antibody technology (2). Similarly, the decision by Kunkel to submit the myeloma proteins to a careful immunologic analysis, designed to identify the determinants that characterize them individually, and as a distinct group, resulted in a series of fundamental contributions to our understanding of the immunoglobulin molecules. In 1955, using this pioneering approach, Kunkel demonstrated the unique idiotypic determinants of human myeloma proteins and of antibodies (Slater et al., 1955; Kunkel et al., 1963). The discovery of distinctive idiotypic determinants on antibodies (described independently by Oudin on rabbit antibodies [3]) was to be the basis for Jerne's network theory of the regulation of immune responses (4).

In 1964, pursuing his investigations of the determinants of myeloma proteins and their genetic control, Kunkel identified the antigenic specificities of the different classes of human immunoglobulins (Grey and Kunkel, 1964; Kunkel et al., 1964; Allen et al., 1964) and the genes controlling the immunoglobulin chains (Gray and Kunkel, 1964; Mannik and Kunkel, 1962; Harboe, Osterland, and Kunkel, 1962). In the course of these fundamental studies, Kunkel discovered the phenomenon of allelelic exclusion of immunoglobulin genes that characterizes this family of molecules and its genes (Harboe, Osterland, Mannik, and Kunkel, 1962). These contributions exemplify one aspect of Kunkel's work, the laboratory analysis of selected clinical material that led to seminal discoveries on the molecular and genetic nature of antibodies. Another, in a sense symmetrical, aspect was the application of the best available immunologic techniques to the study of disease processes. This approach fostered the development of clinical immunology as an independent entity and has been responsible for the training of a whole generation of clinical immunologists. In addition, it led to the discovery in 1957 of the nature of rheumatoid factor (Franklin et al., 1957; Edelman et al., 1958) and the finding of immune complexes of DNA and anti-DNA in the sera and glomerular lesions of lupus patients (Tan et al., 1966; Koffler et al., 1967).

Among Kunkel's other important contributions are the demonstration in 1974 that complement genes, and particularly C2, are linked to HLA (Fu and Kunkel, 1975; Fu et al., 1975); the induction by T cells of in vitro differentiation and immunoglobulin synthesis by human lymphatic leukemia B cells (Fu, Chiorazzi, Kunkel, Halper, and Harris, 1978); the identification of class II major histocompatibility complex antigens on activated human T lymphocytes (Fu, Chiorazzi, Wang, Montazeri, Kunkel, Ko, and Gottlieb, 1978), and, more recently, the demonstration of T cell idiotypic specificities on T cell leukemias, thereby generalizing to the T cells and their receptors Kunkel's earlier observations on B cells (Bigler et al., 1983).

One of the most important and lasting aspects of Kunkel's contribution to immunology and medicine is his record as a teacher and leader of a large group of clinical immunologists who have brought his approach and techniques to their own laboratories. Among those who have greatly benefited from their association with Henry Kunkel are the following (listed chronologically): E. H. Ahrens, A. G. Bearn, R. J. Slater, H. J. Müller-Eberhard, E. C. Franklin, H. R. Holman, G.

M. Edelman, H. Fudenberg, H. R. G. Deicher, T. Tomasi, R. C. Williams, P. J. Lachmann, M. Harboe, M. Mannik, C. K. Osterland, J. H. Rockey, H. M. Grey, J. C. Allen, E. M. Tan, S. D. Litwin, J. B. Natvig, D. Koffler, P. H. Schur, J. D. Capra, W. J. Yount, H. B. Dickler, R. J. Winchester, V. D. Agnello, P. Wernet, Z. Bentwich, J. B. Winfield, N. Chiorazzi, R. G. Lahita, and C. A. Bona.

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