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ELVIN A. KABAT
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A Biographical Memoir by

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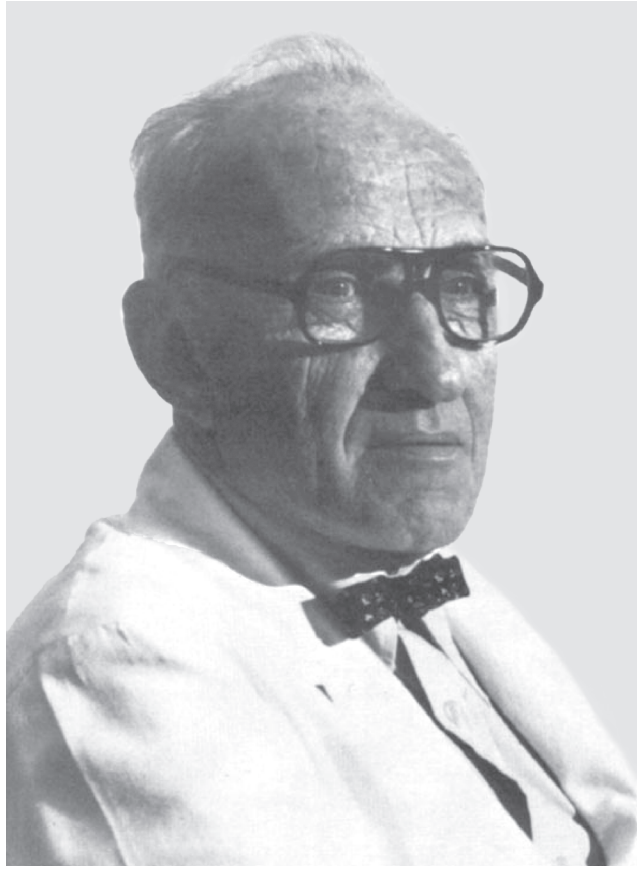

ELVIN A. KABAT

September 1, 1914–June 16, 2000

BY ROSE G. MAGE AND TEN FEIZI

ELVIN A. KABAT, WHO died on June 16, 2000, was a founding father of modern quantitative immunochemistry together with Michael Heidelberger, his doctoral mentor. During his long career the structural and genetic basis for specificity of antibodies was elucidated. It was he who first demonstrated that antibodies are gamma globulins. Although his name is most associated with characterizations of the size and heterogeneity of antibody-combining sites, his contributions to modern biomedicine go well beyond this subject. His work advanced our understanding of fundaments of developmental biology, inflammation, autoimmunity, and blood transfusion medicine. Elucidation of structures of the major blood group antigens, embryonic-stage-specific carbohydrate antigens, and functional carbohydrate markers of leukocyte subsets were either achieved by him and his associates, or made possible through meticulously characterized, invaluable compounds he generously made available to other investigators.

His more than 470 publications span a period of 65 years. Over several decades he was a leading figure in several parallel fields of investigation as is evidenced by the books he authored: *Blood Group Substances–Their Chem-*

istry and Immunochemistry (Kabat, 1956), *Kabat and Mayer's Experimental Immunochemistry* (Kabat, 1961), *Structural Concepts in Immunology and Immunochemistry* (Kabat, 1976), and the series of five editions of *Sequences of Proteins of Immunological Interest*. The most recent edition of *Sequences* appeared in 1991 (Kabat et al., 1991), after which a website was established. The printed and subsequent Web version was a pioneering effort that preceded the current GenBank database. Indeed, Kabat was also instrumental in urging the National Institutes of Health to support a national DNA sequence database and the development of sequence manipulation software (Lewin, 1982).

When one of us (R.G.M.) was in the Kabat laboratory as a graduate student (1957-1962), it was located in the Columbia Presbyterian Hospital's Neurological Institute. This came about because Kabat was hired by Columbia University to conduct immunochemical studies of neurological diseases, including the human autoimmune disease multiple sclerosis. He made seminal contributions to the development of an animal model of multiple sclerosis (Kabat et al., 1946, 1947, 1948) and of a diagnostic test based upon elevated levels of gamma globulin he found in cerebrospinal fluid (1948). The immunochemical measurements of patients' gamma globulin levels were done in the Kabat laboratory for 30 years. The experimental autoimmune (or allergic) encephalomyelitis (EAE) model is still widely used today.

Both of Kabat's parents arrived in the United States from Eastern Europe toward the end of the nineteenth century. Elvin was born on September 1, 1914. His father and two uncles had changed their last name from Kabatchnick to Kabat in 1908, possibly because they had a dress manufacturing business that they named Kabat Bros. The business prospered until 1927, when changing economic conditions

led to bankruptcy and a period of difficult times for the family. Those of us who worked in Elvin's laboratory were made aware of his experience during the difficult times that extended through the Great Depression. Elvin was always very careful with laboratory expenditures. Rose Lieberman, a long-term member of the Laboratory of Immunology at the National Institute of Allergy and Infectious Diseases and fellow graduate student of Kabat at Columbia, used to tell one of us (R.G.M.) that she and Elvin shared one can of soup for lunch.

Elvin entered high school at the age of 12 and completed it in three years, thus he entered the City College of New York at 15, graduated with a major in chemistry in 1932 at the age of 18, and in January 1933 was already working in Michael Heidelberger's laboratory doing routine laboratory tasks at Columbia University's College of Physicians and Surgeons. The opportunity to work in the Heidelberger laboratory came through Heidelberger's wife, Nina Heidelberger, a customer of Kabat's mother who was selling dresses to help make ends meet. Once Heidelberger had agreed to give him a job, Kabat was able to start work on his Ph.D. in the Department of Biochemistry, taking most courses at night. Although originally hired to assist with routine laboratory maintenance, he was soon working on quantitative agglutination (1936) and precipitin (1937) reactions and completed his Ph.D. in only four years. A major conclusion emerging from this work was that the same antibody molecules could agglutinate particulate antigens, such as pneumococci bearing capsular polysaccharide and precipitate soluble pneumococcal polysaccharide (1936).

From his own statements in autobiographical memoirs (Kabat, 1983, 1988), it is quite clear that he wanted to go to medical school, but this was not possible without scholarship support. His career path brought him back to the

medical schools he applied to; he was briefly on the faculty of Cornell (1938-1941) and then for the majority of his career at Columbia, where his impact on the progress of biomedical research was probably far greater than it would have been if he had practiced clinical medicine himself. He taught and strongly influenced generations of medical students, graduate students, and postdoctoral fellows. Thus, in addition to his own contributions to advances in basic immunology and clinical medicine, he helped to prepare many future leaders in clinical research as well as in basic fields as diverse as glycobiology, immunogenetics, and bioinformatics.

Michael Heidelberger suggested that Kabat do postdoctoral training with Arne Tiselius and Kai Pederson in the Svedberg laboratory in Uppsala, Sweden, where the new methods of ultracentrifugation and electrophoresis were being developed. Elvin received a postdoctoral fellowship sponsored by the Rockefeller Foundation. Antisera against pneumococci, purified pneumococcal carbohydrate antigens, and some purified antibody fractions (1938) from various species, including horses, pigs, rabbits, a cow, and a monkey, were prepared and shipped ahead to Uppsala. There, working with Pedersen, Kabat found by ultracentrifugation studies the 18 or 19S antibody (now known as IgM) in horses early after immunization, and the heterogeneity of molecular weights of antibodies from hyperimmunized horses and other species (Kabat and Pederson, 1938; Kabat 1939). Working with Tiselius (1939), he conducted the groundbreaking electrophoresis experiments that first demonstrated that anti-ovalbumin antibodies in sera of hyperimmunized rabbits were gamma globulins (IgG). Before returning to New York to take up a position in the Pathology Department at Cornell University Medical College, Kabat started what was to be a pattern throughout his life: establishing

friends and contacts in laboratories around the world. Not yet 24 and just completing a one-year postdoctoral fellowship, he managed to visit many leading lights in biochemistry at that time, including Linderstrom-Lang in Copenhagen, Hans Krebs in Sheffield, and numerous others in laboratories in London, Cambridge, Birmingham, Leyden, and Amsterdam (listed in his 1983 autobiography [Kabat, 1983, p. 8]).

In 1942 Elvin married Sally Lennick, a young and talented art student from Canada. Sally made those of us who worked with Elvin feel more like family, which helped to counterbalance the demanding standards and pace of life in the Kabat laboratory. She sketched beautiful portraits of their young sons and once Jonathan, Geoffrey, and David were older she traveled extensively with Elvin, sometimes sketching local scenes or portraits of cooperative participants at scientific meetings.

Kabat's work on the structures of the blood group antigens began in 1945. It is interesting to recall the background to his entry into this field, where his contributions have been spectacular. As Kenneth O. Lloyd and one of us (T.F.) wrote in Kabat's obituary published in the *Glyconjugate Journal* (2000) and *Glycobiology* (2001), he was working with Michael Heidelberger on quantitative immunochemistry of bacterial polysaccharides, when he read a paper published by Karl Landsteiner and Merrill Chase in 1936 in the *Journal of Experimental Medicine* describing the presence of blood group A substance in commercial pepsin. Kabat was stimulated by this report, knowing how little antigenic material can be obtained from red cells. He suggested to Heidelberger that they might "do some quantitative precipitin tests" using this soluble material and human anti-A sera. His mentor's response was that this was a good problem for him to pursue as an independent investigator. Thus, Kabat's

interest in the blood group antigens remained latent, only to be rekindled by a proposal by Ernest Witebsky and colleagues during World War II that soluble A and B substances from hog and horse stomachs might be added to group O blood to neutralize the anti-A and anti-B to make it a better universal donor blood. Some of the preparations were not meeting specifications in that they induced anaphylactic shock in guinea pigs, and Witebsky suggested to Kabat that he look into the question. Kabat applied for a contract from the Office of Scientific Research and Development, which he received very late in the war, in 1945, shortly before V-E day.

By the time Elvin Kabat's studies on the blood group antigens were launched, there had been some important developments. Walter Morgan and colleagues in the United Kingdom had shown that large amounts of blood group substances occur in human ovarian cyst fluids, and they had developed methods for their isolation. Ernest Witebsky and colleagues had succeeded in producing high titer anti-A and anti-B sera by immunizing volunteers with hog A and horse B substances isolated from gastric epithelia. Thus, the scene was set for quantitative precipitin assays of the blood group antigens. These assays, coupled with hemagglutination assays, served initially to monitor the purification and characterization of the blood group substances, and their partially hydrolyzed forms. Later on they were important in identifying the oligosaccharides that contained the blood group determinants in the following two decades; the biochemical basis of the major blood group specificities was elucidated by Kabat's group in parallel with Walter Morgan and Winifred Watkins at the Lister Institute in London.

In the first phase of this pioneering immunochemical work with blood group-active polysaccharides (mucins) of human and animal origins, it emerged that there were some

similarities in these highly complex substances, and also differences between those of differing A, B, and O (H) types. By mild acid hydrolysis, immunoreactivities were revealed with horse antibodies raised to pneumococcus type XIV polysaccharide. This indicated the presence of common sequences in the backbone regions of their oligosaccharide chains. The other major conclusion was that the "structural groupings" associated with each of the three blood group types and the type XIV cross reactivity were distinct. By 1966 the chemical structures of these major blood group antigens, as well as the blood group Lewis^a (Le^a) and Le^b, had been determined, and a composite structure for the carbohydrate chains on the epithelial mucins that bear the various blood group determinants had been proposed; the genes (coding for glycosyltransferases) involved in the biosynthesis of the blood group antigens were anticipated (Lloyd and Kabat, 1968).

The significance of this work extends beyond our current understanding of the biochemical basis of the major blood group antigens. This work opened the way to the elucidation of several blood-group-related carbohydrate antigens, later to be referred to as carbohydrate differentiation antigens, whose expressions change sequentially from the earliest stages of embryogenesis right through differentiation events in adulthood, and also in oncogenesis. Among these are the I and i antigens expressed on specific parts of the backbones of this family of oligosaccharides, and the Le^x and Le^y antigens expressed as capping structures (Feizi, 1985). The latter sequences were designated new gene products by Lloyd and Kabat (1968) when first discovered on the epithelial mucins. The foundations had been laid for understanding the roles of members of this family of carbohydrate antigens as ligands for carbohydrate-binding receptors. Notable examples are the roles of the Le^x-related and

Le^a-related oligosaccharides on glycoproteins and glycolipids as recognition elements for the leukocyte-endothelium adhesion molecules, selectins, which play a crucial role at the initial stage of leukocyte recruitment in inflammation (Feizi, 2000).

In a notarized document dated August 1, 1996, entitled "The Care and Maintenance of the Elvin A. Kabat Collections of Purified Carbohydrates and Other Materials at Columbia University" Kabat appointed his last graduate student, Denong Wang, to be the curator of research materials, including in addition to the carbohydrates, "antibodies, cell lines and other related materials." In the second paragraph of this document he states, "The collection of polysaccharides has been in the possession of Professor Elvin A. Kabat and used by his graduate students and collaborators since 1932 when Dr. Kabat was working and collaborating with Professor Michael Heidelberger. Some of the materials were prepared in Prof. Karl Landsteiner's laboratory while he was in Austria and later at the Rockefeller Institute for Medical Research." Those of us who worked in Kabat's laboratory remember well that some of the most valuable of these materials were kept locked in a safe. It is likely that the safe dates back to the days of World War II, when Kabat worked on several projects related to the war effort to improve methods of immunization and protection against potential biowarfare agents. The research was sponsored by the Office of Scientific Research and Development (OSRD) and the National Defense Research Committee (NDRC).

In addition to immunochemical studies of meningococcal meningitis that included immunization of medical student volunteers with meningococcal polysaccharide (Kabat et al., 1947), Kabat lists himself as "chemist" on an NDRC project. This supported the studies of ricin by Kabat and Heidelberger. A paper entitled "A Study of the Purification

and Properties of Ricin" by Kabat, Heidelberger, and Bezer (1947) presents a summary of "a portion of a study carried out during 1943-45 in consultation and collaboration with other laboratories engaged in parallel investigations." The fears of its use for biowarfare (by the Nazis during World War II) are sadly still with us 60 years later in the form of the current anxiety about bioterrorism. Theodor Rosebury and Kabat also prepared a classified report on potential bacterial and viral biowarfare agents. This was declassified and published in the *Journal of Immunology* after the war (Rosebury and Kabat, 1947).

Kabat was involved in additional national and international endeavors after World War II. He served on several different advisory panels for the National Research Council, the Office of Naval Research, and the National Science Foundation, as well as for private foundations, including the National Multiple Sclerosis Society, American Foundation for Allergic Diseases, New York Blood Center, Roche Institute of Molecular Biology, Institute of Cancer Research, and Gorgas Memorial Laboratory, Panama. He was a member of the World Health Organization Advisory Panel on Immunology from 1965 to 1989. A succinct article by Kabat (1986) entitled "A Tradition of International Cooperation in Immunology" describes the World Health Organization's efforts starting in 1963 to establish research and training centers in immunology in developing countries. Kabat traveled several times to Africa, helped to select and establish the first such center in Ibadan, Nigeria, and helped to monitor its progress. His own longtime technician Ada Bezer later worked for the WHO and assisted in the running of the Ibadan laboratory and in the training of students and researchers who came to work there.

His interest in developing quantitative methods to study allergic reactions (Benacerraf and Kabat, 1949, 1950) led

to an invitation to serve on the Subcommittee on Shock of the National Research Council. Dextran had been developed in Sweden for use as a plasma expander but administration had led to some severe allergic reactions. In a series of experiments Kabat proved that the allergic reactions were due to immune response to the dextran itself rather than to contaminants (1953). Most dramatically he immunized himself and then performed a skin test on himself (which proved positive) and on a control subject (negative) at a subcommittee meeting. This discovery of the antigenicity of dextran was the start of a long series of studies of the size and heterogeneity of the antibody-combining site using the very simple and well-defined dextrans and oligosaccharides of defined length as inhibitors of the precipitin reaction. Antisera were raised in medical student volunteers (and graduate students, including R.G.M.). Studies of the inhibition of the precipitin reaction between linear α-(1→6) linked dextran and human antidextran antibodies by members of the isomaltose series of oligosaccharides between 2 and 7 monosaccharide units in length demonstrated that the upper limit of the combining site size was equivalent to a hexasaccharide (isomaltohexaose) (1957, 1960). This was later extended to rabbit antibodies raised against whole dextran-bearing *Leuconostoc mesenteroides* (Mage and Kabat, 1963a).

Before the advent of hybridoma-derived monoclonal antibodies, human antidextran antibodies were fractionated by differential elution with oligosaccharides of different length (Schlossman and Kabat, 1962) and later by differential precipitation of antibodies elicited to branched dextrans; first precipitating antibodies specific for α-(1→6); and then for α-(1→2) or (1→3)-linked glucose residues (Dorner et al., 1967). A classic paper in the series on studies of human antibodies with Henry G. Kunkel's laboratory (1968) de-

scribed heavy chain subgroups (isotypes), light chain types, and Gm allotypes found in fractionated human antibodies, including antibodies from subject 1 (Elvin Kabat) to dextran, levan, diphtheria toxoid, and tetanus. The studies suggested that some of the fractionated samples were of somewhat limited heterogeneity. The sharing of the Louisa Gross Horwitz prize for outstanding basic research in the fields of biology or biochemistry by Heidelberger, Kunkel, and Kabat in 1977 may in part have been because of this collaborative work.

In further studies of fractionated and purified antibodies from subject 1 (Kabat again) (1975), isoelectric focusing studies confirmed that fractionated antidextrans, as well as antilevan, and anti-blood-group A, could be quite restricted or possibly monoclonal. The most important finding in this paper, from quantitative inhibition studies of both the fractionated antidextrans and mouse myeloma proteins with specificity for dextran, was that antibodies could react at nonterminal locations along a linear α-(1→6)-linked dextran chain. Kabat referred to these as "groove type" combining sites and in lectures would sometimes say that the polysaccharide chain was bound to the antibody "like a hot dog in a roll." Other binding sites that recognized only terminal nonreducing ends were referred to as "cavity-type sites." When hybridoma technology became available, Kabat's laboratory conducted further detailed analyses of monoclonal antibodies of defined specificity to both linear and branched dextrans (1981). These studies continued through the next decade (Wang et al., 1991).

The finding of groove-type antidextran combining sites also helped to explain earlier studies of precipitating antibodies to type III pneumococcal polysaccharide (SIII), a largely linear polymer of the disaccharide cellobiuronic acid (Mage and Kabat,1963b). Before embarking on these stud-

ies, one of us (R.G.M.) had to generate precipitin curves using as antigen an acid hydrolyzed fraction of SIII that had been prepared by Michael Heidelberger and a horse anti-SIII, produced before I was born. After I generated a set of precipitin curves and showed them to Elvin, he produced the curve done by Heidelberger in 1935. The curves generated with the same materials more than 20 years later, superimposed. I learned the evening after I told this story at the memorial symposium held for Elvin at Columbia in November 2001 (<http://www.columbia.edu/~dw8/kabat>) that a student who worked with Elvin many years later was given antidextran antibodies that I had studied and was required to prove that he could reproduce the precipitin curves I had generated.

As a complement to his studies on anticarbohydrate antibodies, Kabat was interested in the specificities of plant and animal lectins, which also recognize sugar units. Other investigators were already engaged in studies on the specificities of lectins. Kabat was able to use his extensive collection of polysaccharides and oligosaccharides to analyze their ligands in greater detail. These studies often led to new insights into the specificities of the lectins and opened the way for their use as specific reagents for immunochemical and immunohistological studies. Among the lectins studied were those from *Helix pomatia, Dolichos biflorus, Griffonia simplicifolia*, several marine sponges, and the chicken hepatic lectin (the last with Gilbert Ashwell of the National Institutes of Health).

In 1974 the Kabats arrived to spend a sabbatical year at the NIH. Elvin had received the prestigious appointment as an NIH Fogarty scholar. He quickly became an important part of the NIH immunology community and developed many friendships, including with David Davies and Eduardo Padlan. Eduardo built a model based on a protein sequence

of purified monoclonal rabbit anti-SIII published by J.-C. Jaton and the solved crystal structure of mouse myeloma protein McPC603 from the Davies laboratory. In this model a hexasaccharide neatly fits across the combining surface of the antibody. This gave us all great pleasure for, as with dextran, we had concluded that the combining sites of antibodies to this more complex polymer had an upper size limit of a hexasaccharide (Mage and Kabat, 1963b). Although a picture of the model was never published in a formal paper, it appeared on the cover of *P&S, The Journal of the College of Physicians and Surgeons of Columbia University* (vol. 5, no. 3, 1986).

A most important result of the one-year sabbatical was that at its end Elvin remained a member of the NIH community for the rest of his career, until failing health interfered with his ability to travel. He became an expert consultant for the National Cancer Institute, later for NIAID and the Office of the Director, and on most weeks spent Saturday afternoons through Tuesdays at NIH and the remainder of the week at Columbia. This came about because Kabat had been compiling antibody variable region sequences with Tai Te Wu and seeking to understand which portions of the sequences contributed residues that made contact with antigens. William Raub of the NIH Division of Research Resources brought the PROPHET computer system to his attention and introduced Kabat to Howard Bilofsky of Bolt, Beranek, and Newman. This was the start of the database referred to earlier that was eventually published in five printed editions starting in 1976, when only amino acid sequences of variable regions were included, and extending through a three-volume fifth edition. It was now entitled "Sequences of Immunological Interest," because it included sequences of variable and constant regions of antibody heavy and light chains, including codons of those

amino acid sequences that had been deduced mainly from cDNA clones. In addition, the database now included amino acid sequences and corresponding codons of a variety of other genes of the immune system, including T-cell receptors and transplantation antigens.

Although the Kabat database of proteins of immunological interest is no longer supported by government funds, it is currently available at <http://kabatdatabase.com> due to efforts of George Johnson. It is uncertain how long it will remain available; it is maintained with funds from subscribers, and current funds barely offset the maintenance costs. Andrew Martin has a valuable searchable "Simple Interface to the Kabat Sequence Database," called KabatMan at <http://www.bioinf.org.uk/abs/simkab.html>. This includes only immunoglobulin sequences that have at least 75 residues, so the database contains essentially only complete light or heavy chain sequences. The database version is that of July 12, 2000. It contains 6,014 light chain and 7,895 heavy chain sequences of which 2,140 form complete antibodies.

As early as 1967 Kabat was publishing analyses of variable regions of human and mouse Bence-Jones proteins (immunoglobulin light chains) (Kabat, 1967). After he enlisted the help of T. T. Wu, who had a background in mathematics, computers, and biophysics, they rapidly completed an extensive compilation of available light chain sequence information and published in the *Journal of Experimental Medicine* the first variability plot in a landmark 40-page paper (1970) that defined variability as the ratio of the number of different amino acids at a given position to the frequency of the most common amino acid at that position. The paper suggested that hypervariable regions within antibody variable region sequences would contribute to antibody complementarity. This has been amply confirmed, and

now these regions are referred to as complementarity determining regions (CDR). In his 1988 autobiography (Kabat, 1988, pp. 13-16) he generously credits all the previous investigators whose studies contributed to the initial ideas and data that were crystallized in the 1970 paper and also describes the further refinements that came as further analyses and sequence data became available. Kabat had thought of submitting this paper to the *Journal of Theoretical Biology*. When he happened to mention this to Henry Kunkel, there was no doubt in the mind of the then editor in chief of the *Journal of Experimental Medicine* that the paper should be submitted to this journal. It was the privilege of one of us (T.F.), who was working as a guest investigator simultaneously in the Kabat and the Kunkel laboratories, to carry the submission from Columbia Medical Center to Rockefeller University. It is an interesting experience to revisit this paper more than 30 years after it was published and realize that it was written before immunoglobulin class switching and VDJ recombination had been discovered and before any maps or sequences of immunoglobulin germline genes were available. It already hypothesized that there might be some "episome"-like introduction of information into variable region gene sequences. Nine years later (1979) a formal paper supporting the idea of minigenes was published. Although the minigene hypothesis in its original form was not correct, the discovery of VDJ recombination revealed that the J genes accounted for the minigene-like behavior of the fourth framework region of variable regions. A 1980 paper (Kabat et al., 1980) provided evidence indicating independent assortment of framework and complementarity-determining segments of the variable regions of rabbit light chains. Now, from examination of rabbit germline Vκ sequences it appears that what they observed was due both to gene conversions that occurred during evolution of the multiple Vκ

genes and to gene conversion-like changes that accompany somatic expansion and diversification of rearranged VκJκ sequences in rabbit splenic germinal centers (Sehgal et al., 2000).

Elvin Kabat was elected to the National Academy of Sciences in 1966, the same year that he served as president of the American Association of Immunologists. He received many prizes, honors, honorary degrees, and invitations to present named lectures. Perhaps most important to him was the award of the National Medal of Science in 1991. As William Paul and one of us (R.G.M.) wrote in his obituary published in *Nature* (2000),

> He valued this honor greatly, particularly because of the difficulties he had in the 1950s when the National Institutes of Health cravenly terminated his grants as fallout of the politics of the McCarthy era. Fortunately, the Office of Naval Research and National Science Foundation continued to support him. Kabat regarded the Medal of Science as recognition of a career-long record of accomplishment, and as a personal vindication.

Less well recognized in scientific circles were Kabat's strong beliefs in justice and the defense of what was right whether politically correct or not.

Throughout his career at Columbia, Kabat had three or four parallel lines of investigation ongoing at any given time. He was a chemist by training, a pioneer in the field of protein chemistry, and one of the founding fathers of immunochemistry. His contributions to understanding the nature of the antibody combining site and of antibodies that cross react with different carbohydrate antigens (1942), carbohydrates and DNA (1985, 1986), or DNA and peptide mimics are highly relevant today, for example, as we seek better understanding of the role of infectious organisms in initiating and exacerbating autoimmune diseases. It is remarkable that he also became a major figure in the fields of glycobiology and database development. The Wu-Kabat

variability plot is still used to analyze sequence data not only of immunoglobulins but also of T-cell receptors and even of rapidly evolving viral sequences. As Donald Marcus and Stuart Schlossman wrote in the 2001 Kabat obituary in the *Journal of Immunology,* "His passion for science, integrity and high standards made him a demanding taskmaster, and his critiques of experimental data could be unsparing. His former trainees enjoyed getting together at international meetings to reminisce about their experiences in his laboratory and what it meant to be 'Kabatized'." According to Schlossman and Nobel Laureate Baruj Benacerraf, "To be 'Kabatized' and survive meant you could do well anywhere. . . Kabat's wonderful sense of humor and his talent as a raconteur leavened the serious atmosphere of the laboratory. Scientists trained in his laboratory carried with them a model of how science should be performed, and his trainees maintained enduring personal and professional relationships with him."

IN PREPARING THIS memoir we were greatly assisted by Kabat's own detailed autobiographies (Kabat, 1983, 1988), as well as by memories of our close association with him during our training in his laboratory. In addition, one of us (R.G.M.) remained in close contact with him throughout his tenure as a consultant to NIH. We thank Denong Wang for providing a copy of the notarized document appointing him curator of Kabat's research materials. We also gratefully acknowledge critical suggestions and comments from family members and from colleagues, including Gilbert Ashwell, George Johnson, Ken Lloyd, Nancy McCartney-Francis, Mike Mage, David Margulies, Donald Marcus, Barbara Newman, William Paul, and Tai Te Wu, as well as permissions from the *Glycoconjugate Journal* to publish excerpts from the obituary of Elvin Kabat and from the *Annual Review of Immunology* to republish the photograph of Elvin Kabat that appeared in part I of his autobiography (1983). It is reprinted with permission from the *Annual Review of Immunology,* Volume 1 ©1983 by Annual Reviews. We thank Shirley Starnes for expert editorial assistance.

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