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WILLIAM HAY TALIAFERRO

1895—1973

A Biographical Memoir by

DAVID W. TALMADGE

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WILLIAM HAY TALIAFERRO was born prematurely on February 10, 1895 in Portsmouth, Virginia. His doctor considered his survival remarkable and gave the credit to his mother, Mary Watkins Leigh, for her solicitous care. He was a member of the ninth generation of Virginia Taliaferros and was descended from Robert (1626–1688). The name is English, and it is pronounced Toliver.

Both sides of his family were Virginia aristocrats who had become impoverished by the Civil War. Both grandparents were physicians, but his father was barred from the profession by a hunting accident that resulted in the loss of his right hand. With this background it is not surprising that William's boyhood ambition was to be a physician.

William attended public school in Portsmouth until the age of ten. He then went to Sunnyside Seminary, near Clarksville, Virginia, for three years. This finishing school for girls was run by three Carrington great-aunts who permitted William and several other boys to attend as day students. The boys added zest to the education of the girls by bringing snakes, frogs, bugs, and other novelties into the classroom. As far as his studies were concerned, William excelled in arithmetic, but he never could spell, although he took to Old English and enjoyed looking up the derivation of words.

Once he confided to Karl Lashley, his closest friend at Hopkins and thereafter, that he never knew whether "separate" had 2 *e*'s or 2 *a*'s in its middle, whereupon Karl replied that he never could decide whether "which" had a *t* in it or not.

In 1908, at the age of thirteen, William received a scholarship to Norfolk Academy in Norfolk, Virginia. This private preparatory school had a distinguished history. There he was grilled in the old-fashioned studies of mathematics, English, and history. He took all the science that was offered, but this was limited to the most elementary physics and chemistry. He was not interested in sports and spent his free time reading. He received the Class Prize in 1910 and the Ingram Prize in 1911.

William was shy and timid as a boy and was protected at times from the school bullies by a stronger older brother. This shyness carried over into adulthood as a remarkable gentleness that endeared him to his friends and students. Shyness did not suppress an early resourcefulness. To assure funds for his later education, William sold eggs from a pedigreed flock of hens. He devised an ingenious method of feeding them during classroom hours at Norfolk Academy. He turned an alarm clock on its side and balanced a weight on the clapper. At noon, the weight dropped and upset a box of feed. He always remembered those Plymouth Rocks with pleasure because of "their upturned heads and alert eyes around noontime."[1] Unfortunately, he later developed an allergy to many animal danders that kept him out of the animal quarters.

From the fall of 1911 through the spring of 1915 William attended the University of Virginia. In his junior and senior years, he had teaching assistantships under Dr. William A. Kepner, who not only took him on innumerable field trips

[1] W. H. Taliaferro, *Annual Review of Microbiology*, 1968.

and gave him valuable teaching experience but replaced his ambition to study medicine with a lifelong love of zoology. Zoology must have been a little-known profession in those days. When William announced at home that he had decided to be a zoologist, his brother remarked, "Good Lord, William, are you going to be a zookeeper?"[2] While at the University of Virginia, he published three papers with Dr. Kepner on the sensory epithelium of *Microstoma caudatum*, the organs of special sense in *Prorhynchus applanatus*, and the reactions of *Amoeba proteus* to food. William graduated from the University in 1915 with a bachelor of science degree after election to Phi Beta Kappa. He was invited to join the Raven Society of the University in 1944.

While at the University of Virginia, William was impressed with a book by Dr. Herbert S. Jennings of the Johns Hopkins University, entitled *Behavior of the Lower Organisms*. He determined to go to Hopkins and study under Jennings. When he arrived there in the fall of 1915, he found that Jennings had changed his field to genetics and was placed under the guidance of Dr. Samuel Mast. Nevertheless, he attended all the lectures given by Dr. Jennings and those by Dr. Burton Livingston on plant physiology. From the latter he learned to use porous filters that were useful in his research on antibodies to trypanosomes.

William's training in genetics led to the publication of a paper with John Huck on the inheritance of the sickling of human red cells in several Negro families. He and Huck concluded that this phenomenon, later called the sickle-cell trait, is inherited as a single, Mendelian dominant gene (S) that is not sex-linked. Others later showed, on the one hand, that the homozygote recipients of two S genes suffer from severe sickle-cell anemia, and, on the other, that the heterozy-

[2] *Ibid.*

gote carriers of only one S gene demonstrate the sickle-cell trait *in vitro*, are free of the disease, and are resistant to the lethal effects of the virulent African malarial parasite, *Plasmodium falciparum*. This disease-host relationship has become a model for the study of genetics and evolution because it shows how an unfavorable gene may be advantageous under particular conditions.

While at Hopkins, William joined the Beta Theta Pi Fraternity. The boys christened him "Tolly," an affectionate name he carried the rest of his life. He was never called Bill. The boys also taught him to play poker and bridge and took him to the Saturday burlesque shows at the old Holiday Street Theatre. It must have been there that he started to accumulate the vast stock of stories for which he was famous.

In the summer of 1917, William was invited to assist in a course on invertebrate zoology at Woods Hole, Massachusetts. There he met Lucy Graves, a Yankee of *Mayflower* descent, who later became his wife. She had just graduated from Goucher College with a bachelor of arts degree after election to Phi Beta Kappa. Since William and Lucy were each engaged to someone else at the time, they thought it safe and pleasant to date each other. In any case, the Goucher table where Lucy was a student must have received an unequal share of the young instructor's time because Dr. Allee is quoted as remarking one day, "Taliaferro, in previous years, the Goucher bunch have always seemed intelligent, but this year they seem to need all your attention while I have to instruct the rest of the class."[3]

Tolly volunteered for service in the army in the fall of 1917 and was assigned to the Division of Chemical Warfare at Yale. While there he finished his thesis, passed his oral examinations, and received his Ph.D. from Hopkins in the

[3] L. G. Taliaferro: personal communication.

spring of 1918, at the age of twenty-three. This accelerated program was made possible by his exceptional training at the Norfolk Academy (he was excused from freshman English and mathematics when he entered the University of Virginia) and continuous attendance at the University of Virginia summer and winter. His thesis was on reactions to light in *Planaria maculata*, a small flatworm, with special reference to the function and structure of the eye. The experiments had been well-planned and carried out at the University of Virginia. The technique and analysis of the results were far in advance of their time.

When Tolly and Lucy left Woods Hole in 1917, they never expected to see each other again, but they continued to correspond. Then, in 1918, Lucy, who was abstracting German articles on gases in the Department of Chemical Warfare, was transferred to New York City. Tolly, who was assisting in a research program on respiratory gases under Dr. Yandel Henderson at Yale, had to go to New York City frequently to get pyrex glass blown for intricate assemblies of equipment. There he looked up Lucy to take her to dinner. His private's pay was stretched to capacity! Their friendship, however, blossomed to the extent that they became disengaged from their financées and engaged to each other. They were married in June 1919.

In the spring of 1919, when his stint in the army ended with the rank of second lieutenant, Tolly was awarded a Johnston Scholarship at Hopkins, but declined it to accept a position under Dr. Robert Hegner in the Department of Protozoology and Medical Entomology in the newly established School of Hygiene and Public Health at Hopkins. While there, the book by Hegner and Taliaferro on *Human Protozoology* appeared. Also, Lucy passed her oral examinations and received her Sc.D. with a thesis on avian malaria. Thus, she became a full member of the Taliaferro

team, and the names Taliaferro and Taliaferro appear on many of the more than 100 contributions to science that are mentioned here. They were a perfect team—each respected the other for what each did best. Lucy always said that Tolly breezed in on the express with ideas and questions, and she and one or two assistants arrived later on the freight loaded with experimental data involving injections, blood smears, bleedings, autopsies, and tests galore. Then, as a team, they graphed, tabulated, arranged, rearranged, described, and summarized the results for publication. Usually all three processes were occurring simultaneously on different subjects: a manuscript was being readied for publication on old project one, experiments carried out on intermediate project two, and new ideas were being dreamed up for new project three. Some of the dreaming became sidetracked, delayed, or wrecked by sheer lack of time and energy.

William and Lucy also bought a house in Roland Park, a suburb of Baltimore, expecting to be settled there for years. It was not to be. In 1924 William was invited by Dr. Edwin O. Jordan to join the Department of Hygiene and Bacteriology at the University of Chicago. Three years later he was made a full professor. There he and Lucy remained for thirty-six years and did the bulk of their life's work. During that time they lived in one apartment for eight years and in a second one for twenty-eight years! Their research activities centered around host-parasite relationships and the mechanism of antibody formation with hemolysin formation as a baseline.

Although Tolly had never worked on parasites before, his newly found interest in genetics led him to study variability in *Trypanosoma lewisi*, a blood-inhabiting parasite of the rat. Frequent blood smears were made throughout infections lasting a month or more. Number counts and camera lucida drawings from such smears led him to the discovery that the rat not only develops lytic antibodies—the parasite counts fell in

about a week after an initial rise and disappeared later—but also displays a peculiar property of inhibiting parasite reproduction—initial variability of the parasites fell near zero in ten days. Later, when he determined that this factor was an antibody, he called it ablastin. He always considered this discovery his greatest achievement, and it was a recurring theme for study throughout his life. In fact, the last research he published in 1971 with one of his students, Dr. P. A. D'Alesandro, was on the effect of adenine on innate and acquired immunity in the rat to *T. lewisi*. Others, too, were intrigued by the subject. A workshop on ablastin was arranged by D'Alesandro and was held at Rockefeller University on June 21 through 22, 1973. The resulting papers were published in *Experimental Parasitology* in 1975 (Vol. 38:303–69). Tolly and Lucy also studied other trypanosomes in mice, guinea pigs, rats, and dogs, but the mouse was the only host that yielded a reproduction-inhibiting ablastin against *T. musculi* (=*T. duttoni*). Tolly always had a yen to go to Africa with the hope that there he could study some indigenous hosts of trypanosomes, but the opportunity never materialized. In any case, these relationships made a significant impact on Tolly's own research and led much later to his concentrated attack on hemolytic antibodies.

The unraveling of such host-parasite relationships, combined with an orgy of reading, led to the production of *The Immunology of Parasitic Infections*, published in 1929. When Dr. Carroll Bull of the School of Hygiene at Hopkins, William's immunological consultant of those days, read the manuscript, he commended it, but wrote that the chapters needed summaries! Such a suggestion, though justified, caused consternation and the burning of much midnight oil.

Once the summaries were completed, the Taliaferros took their first trip to Europe. They spent Palm Sunday in London, saw the tulips spread out in bloom like vast oriental

carpets in Holland, and spent a month in Paris with daily trips to surrounding areas. The magnificent cathedrals, with their brilliant red and glowing blue stained-glass windows, were an inspiration. It was a long-remembered episode in their life, which they were not able to repeat until 1956.

The research and the book brought Taliaferro wide recognition. He was invited to give the Harvey Lecture in 1931 and was elected an honorary member of the Harvey Society. He gave the Delamar Lecture at the School of Hygiene and Public Health in Baltimore in 1932. He was elected president of the American Society of Parasitologists in 1933 and received the Chalmers Medal of the Royal Society of Tropical Medicine of England in 1935.

From 1925 on, Tolly was also a member of the Innominates, a collection of about thirty basic scientists at the University of Chicago. They had a dinner meeting once a month at the University of Chicago faculty Quadrangle Club for a talk by one of the members. Afterwards, the men met their wives at the home where the ladies had dined.

During the work on the various trypanosome infections, Tolly was fascinated with the immunological problem of distinguishing between killing and reproduction-inhibiting effects of innate and acquired immune reactions of the host. He and Lucy then began an intensive study of the parasites that cause various malarias. Examination of these blood-inhabiting plasmodia had two distinct advantages. Blood smears could be used not only to obtain number counts of a given infection, but, if taken often enough, would reveal the reproductive cycle because the parasites usually grow and segment synchronously. Such cycles are usually completed every 24, 36, 48, or 72 hours, depending upon the species. The well-known periodic fevers of malaria occur at the time the plasmodia segment in the blood. Many were the evenings Tolly and Lucy carried home canaries, chickens, or monkeys

and parked them in the bathtub in order to make blood smears during the night. This exhaustive and time-consuming search was not very successful as far as the main object was concerned. Parasitic lysis occurred, but no reproduction-inhibiting effect was found in the malarias except for transient ones during the dramatic parasiticidal crises.

The various malarias, however, proved to be invaluable for studying the cellular phases of immunity because plasmodial pigment remains for months as an indigestible marker in host phagocytic cells. This work was started with Dr. Paul Cannon and continued with Drs. William Bloom, Hugh Mulligan, and James Moulder; all were at the University of Chicago except Dr. Hugh Mulligan, who came from England by way of India. The onset of the enterprise was sparked by Dr. Alexander Maximow's work on inflammation following the subcutaneous injection of dyes or India ink. The malaria papers were beautifully illustrated by microscopic camera lucida drawings, and praise for these should be accorded Esther Bohlman Patterson, Tolly's artist from 1935 on.

Examinations of various tissues from infected animals indicated that the plasmodia inhabiting blood cells are phagocytized by macrophages in strategically placed organs, such as the spleen, liver, and bone marrow, and that the macrophages conspicuously increase in number, especially as acquired immunity develops, largely because of the heteroplastic division and development of lymphocytes and monocytes into macrophages. Tolly became convinced that the baffling and, up to this time, largely ignored lymphocytes were important in defense. In 1937 he and Hugh Mulligan coined the appropriate term, lymphoid-macrophage system (LMS), to embrace all cells involved in defense, including the lymphocytes. The term, reticulo-endothelial system (RES),

however, had already been proposed ten years earlier by Aschoff to include cells in defense, although he expressly included lymphocytes. This term was so firmly entrenched in the literature that it is still the preferred term, although it now needs the tacit assumption that lymphocytes are included since the role of lymphocytes in defense is well recognized and their nature is being intensively analyzed.

Taliaferro and Dr. Merrit P. Sarles also found a similar lymphocyte-macrophage relationship in rats experimentally injected subcutaneously with the small nematode worm, *Nippostrongylus brasiliensis*. In this case the strategically located organs, as acquired immunity developed, are the skin, lungs, and intestine.

From all this work and extensive reading, Tolly arrived at the conclusion that cellular reactions in all hosts are similar and stereotyped, whether the invader be living or nonliving, and they only differ superficially because of the invader's size, mode of entrance, and subsequent location in the host.

From 1926 through 1954, the Taliaferros took ten three-month trips for work at centers of tropical disease in Puerto Rico and Central and South America. Three of their journeys were to Panama for intensive work on malaria in monkeys. The Taliaferros always combined a great deal of pleasure with their work on these trips. They swam, played tennis, danced, rode horseback, and crossed the Andes by bus and boat in the justly famous lake region of Chile. Their first airplane trip in 1954 involved crossing the Argentine from Bariloche to Buenos Aires. Publications, in addition to those previously mentioned, included such subjects as a precipitin test in malaria and various tests on equine trypanosomiasis and helminth infections. The trips were subsidized by Dr. W. E. Deeks and the United Fruit Company, the Rockefeller Foundation, and the University of Chicago.

Tolly and Lucy also took lessons in Spanish, but they never got very far. Their assistants were too eager to learn English. Besides, when Tolly was excising a little piece of an already swollen spleen from a malaria-infected monkey for histopathological study, he didn't want to fumble around for the Spanish equivalent of hemostat if the spleen and an unforeseen capillary started spouting blood. Numerous animals were brought back from these trips, such as mice, a dog, agoutis, and monkeys—all containing parasites. On one trip they brought back a cebus monkey for their good friend, Heinrich Klüver of the University of Chicago, who used it for a behavioral study of its ingenious use of tools. This monkey caused a lot of curious amusement to passengers and crew when Lucy took him for his daily walk on ship deck. He was curious too, but apparently not amused. Two graduate students, Drs. Frances A. Coventry and Leslie Stauber, accompanied them on two trips.

In 1939 they called a partial halt to tropical research trips and started spending a month and a half of winter in southeastern Arizona. They made six trips to Los Encinos Ranch on the east side of the imposing Santa Rita Mountains and twenty-two trips to Kenyon Ranch on the west side. Only occasional letters and work on the ever-present unfinished manuscript interrupted these jolly, relaxing respites, which always included a morning horseback ride. In 1968 they took a cruise to Australia and the islands in between and thereafter spent their winters in Hawaii, Key West, or Puerto Rico.

Tolly and Lucy also learned to enjoy the many activities in Chicago's downtown. They attended the theater, movies, and musical programs; for years they had the same balcony aisle seats for the Friday afternoon symphony concerts at Orchestra Hall on Michigan Avenue. After the concerts, they often visited the Art Institute across the Avenue before hav-

ing a martini and dinner at the nearby University Club. Lucy took a day off once in a while for a shopping spree at Marshall Fields. William had frequent nonbusiness lunches at the men's round table at the Quadrangle Club. Their apartment was adequately cared for by dependable and trustworthy Negro women, except for ten years during the depression when they were fortunate to have a young Irish maid, Kathryn Quinn, who learned to serve them and their company beautiful dinners. Scientific reading was a must for them. In addition, Tolly was interested in economics and was a Civil War buff. He especially enjoyed books about Robert E. Lee.

Beginning in 1931, administrative duties claimed an increasing amount of attention and time. Tolly became chairman of the Department of Hygiene and Bacteriology, later known as the Department of Microbiology (1932–60); associate dean (1931–35) and dean of the Division of Biological Sciences, including the School of Medicine (1935–44); advisor to Chancellor Hutchins (1944–47); and associate editor or editor of the *Journal of Infectious Diseases* (1937–60). Tolly's patient gentleness, infallible sense of humor, large stock of stories, and willingness to work long hours all made him an effective administrator, but robbed him of time for the science he loved. He resigned from all administration outside his department in 1948. His attitude was clearly reflected in the reply he gave to Chancellor Hutchins when the chancellor asked him to take two trips in rapid succession. Tolly said this made him feel like Rosie. Rosie announced to the Madam one morning that she was going to resign, and the Madam replied, "Why for heaven's sake, Rosie, you took eleven trips upstairs last week." "Yes'm," replied Rosie, "it's them steps that's wearin' me out."

During World War II, Tolly was the leader of an interdisciplinary group organized to find effective antimalarial

drugs. He and Lucy made a detailed study of the mechanism of quinine and in typical Toliverian fashion were able to insert some order into this complex problem. They concluded: (1) that quinine acts directly without metabolic transformation by inhibiting growth and reproduction of the parasites, (2) that both innate and acquired immunity are useful supplementary adjuncts, and (3) that the spleen assumes two important but antagonistic roles: it decreases the contact of parasite and drug while increasing acquired immunity.

All this work on malaria led in 1949 to a comprehensive review of the lymphoid-macrophage system as the site of general cellular defense and antibody production. In addition, a second classical review appeared on the effects of radiation on the immune response. This paper was originally written as a classified document for the U.S. Atomic Energy Commission and, after being brought up-to-date each time, was published in 1951 as a definitive, much-needed review and in 1964 as a book to which Dr. Bernard Jaroslow was added as an author. These publications served as a background for the subsequent hemolysis work. All work thereafter was subsidized in part by grants from the University of Chicago and the U.S. Atomic Energy Commission.

Tolly continued to receive recognition for his contributions to parasitology. In 1939 he was made the Eliakim H. Moore Distinguished Service Professor at the University of Chicago. He received this news in Florida where he and Lucy were spending a short vacation and it seemed to be one of the biggest surprises of his life. In 1940 he was elected to the National Academy of Sciences and in 1941 to the American Philosophical Society. In 1946 he received an honorary doctor of science degree from the University of North Carolina. In 1947 he gave the Ludwig Hektoen Lecture to the American Society of Bacteriologists in Philadelphia and the Con-

vocation Address at the University of Chicago. His talk was on the need for work in basic science and the dangers of governmental subsidies. In 1949 he received an honorary doctor of letters degree from Temple University, the Mary Kingsley Medal from the Liverpool School of Tropical Medicine, and was made an honorary fellow of the Royal Society of Tropical Medicine and Hygiene of Great Britain. In 1953 he was made an honorary member of the Faculty of Medicine at the University of Chile and in 1954 was elected president of the American Society of Tropical Medicine and Hygiene.

After returning to full-time teaching and research in 1948, Tolly decided to change his research base. He wanted to study antibody synthesis and needed an accurate quantitative antigen-antibody test for a suitable nonreproducing antigen. His aim was to study lysis by itself. None of the parasiticidal antibodies had been quantitatively measured, and the quantitative precipitin test, then in vogue for measuring certain nonliving antigens, was extremely time-consuming. He then, in one of his brilliant guesses, ordered one of the newly perfected Klett-Summerson colorimeters. This machine, he found to his incredulous delight, would measure small differences in the hemoglobin freed from lysed red cells and, therefore, could measure hemolyic antibodies. The simple test he worked out was used to measure a 50 percent hemolytic end point for titers of serums from rabbits injected with sheep red blood cells. The titers then could be partitioned off into linear segments to determine parameters of time and rate of production. The Taliaferros thus obtained from large numbers of rabbits frequent, precise hemolysin measurements that lent themselves to statistical analysis.

In the subsequent work, using normal rabbits as well as irradiated ones, the Taliaferros had the enthusiastic collaboration of their graduate students, Eugene Janssen,

Laurence Draper, Dieter Sussdorf, Peter Stelos, and Bernard Jaroslow. Results accumulated at an astonishing rate. A few of the outstanding findings may be summarized. (1) The hemolysin response to one intravenous injection of sheep red blood cells into rabbits is characterized by a latent period followed by a rapid rise to peak titer and a slower decline. (2) A reinjection of the same amount of red cells stimulates an anamnestic response of somewhat similar intensity but appreciably sooner and at a faster rate. (3) The parameters are modified by the route and amount of red cells injected. (4) Changes in hemolytic titer depend upon concomitant formation and decay. (5) The spleen forms most of the hemolysin, but the bone marrow and lymph nodes continue to produce it at a low level over much longer periods. (6) Two antibodies occur with identical specificity but with different physicochemical characteristics. This finding was a forerunner of the separation of antibodies into five different classes.

The effects on the hemolysin response of X-radiating the whole rabbit or parts of it, such as the spleen or appendix, were also intensively studied. The following conclusions were reached. The hemolysin response is maximally and radically depressed when red cells are injected one or two days after near lethal doses (500–700 R). This conclusion had been previously well-documented in the literature for various immune systems, but findings of recovery and restoration as well as stimulation and enhancement of the response by X-rays were little known or even unknown in any immune system. These conditions were established by pinpointing large and small X-ray doses at different times before and after an intravenous injection or reinjection of a small, standard amount of red cells. Some of their surprising results may be briefly mentioned. (1) Statistically significant results involve a delicate balance of factors. These include variability in host reactivity and the size, time, and location of the dose

of X-rays with respect to the amount of red cells injected into the host. (2) Recovery from X-ray depression occurs but depends upon the injury involved. (3) Normal induction and peak titer can be restored in rabbits irradiated with 400 R one day before the injection of a combination of red cells and certain substances, such as yeast extract, colchicine, or nucleic acid derivatives. (4) The hemolysin response is significantly stimulated when red cells are given to the rabbit just before small doses (25–100 R) or when red cells are given one or two days after the spleen alone is X-rayed with large doses (5,000–10,000 R). (5) The anamnestic response is less affected. (6) Stimulation and restoration of the response were accounted for by the X-ray release of nucleic acid degradation products normally in short supply in the host.

Tolly and I also worked on the synthesis of antibody, but for this we had to resort to the quantitative precipitin test in rabbits during a secondary response to bovine serum albumin. Tolly's knack of devising clever experiments to test key hypotheses was well illustrated by our method of transferring antibody-forming capacity of spleen cells from one animal to another. Either the donor animal or the recipient was given ^{35}S-labeled amino acids. Only when the label was given to the recipient was radioactivity found in its antibody, thus proving that the transferred cells from the donor contained only the machinery for making antibody and not an inactive precursor. We also found, among other things, that long-lived precursors do not occur, that antibody is not stored during the latent period, and that actual synthesis and release of antibody into the serum take less than an hour once the mechanism is operative. These experiments played a key role in the development of cell-selection theories in 1957.

Although the Taliaferros retired from the University of Chicago in 1960, they moved their laboratory about 30 miles west—to the Argonne National Laboratory—and continued

their work until 1969. This move necessitated a whole new life pattern. They had to buy a house and learn to own and drive a car.

Honors for their work continued. In 1960 Tolly received the Condecoracion al Mérito, Bernardo O'Higgins, de Primera Clase, Chile. In the same year, Volume 27, pages 1 through 148 of the *Journal of Infectious Diseases* was dedicated to him and contained papers solely by his students and associates. In the same year there was a testimonial luncheon and volume of letters given him by his students and associates. The following letter from that volume, written by Robert M. Hutchins, who was president and then chancellor of the University of Chicago from 1929 through 1951, indicates the esteem in which Tolly was held by his associates.

> I have known William Taliaferro for more than thirty years. From the start I was impressed by his scientific integrity and his administrative dexterity. I need not add that I was also impressed by the charm of his personality and the wit of his conversation. Here you have the ideal university man. We shall not look upon his like again.

Not all the honors were without work. In 1960 Taliaferro and Dr. J. H. Humphrey of England were asked by the Academic Press to start *Advances in Immunology*. They guided Volume 1 in 1961 and Volume 2 in 1962 through publication and then entrusted the chore to others. From 1956 on, Tolly was invited to give various opening or closing addresses at symposiums or international congresses at Oak Ridge, Rutgers, Stockholm, London, and Rome, as well as lectures at the Naples Zoological Society, the Pasteur Institute, and the University of Glasgow. Other honors also followed. In 1961 he was elected an honorary member of the British Society of Immunology. An international symposium on "The Effects of Ionizing Radiation on Immune Processes," honoring him and Hugo Frick, was sponsored by the Atomic Energy Com-

mission and the University of Kansas and was held at that university on 5-7 September 1961. In 1962 he was given the Pasteur Award by the Society of Illinois Bacteriologists and delivered the Gehrman Lecture at the University of Illinois Medical School. In 1968 he was asked to write his autobiography for Volume 22 of the *Annual Review of Microbiology*. This prefatory chapter outlines his approach and contributions to science. In 1969 and 1970, Volumes 1 and 2 of *Immunology to Parasitic Animals* were dedicated to him, and he wrote the foreword. These two volumes were a direct descendant of Tolly's 1929 *The Immunology of Parasitic Infections*. They contained many chapters by former students and associates and were a fitting acknowledgment of and climax to his work on host-parasite interrelations.

In 1969 Tolly and Lucy celebrated their golden wedding anniversary and retired, although several more of their papers appeared after that date. William Taliaferro died on December 21, 1973.

Tolly has been adequately recognized for his contributions to parasitology. *The Immunology of Parasitic Infections*, published in 1929, was a milestone in the physiological approach to parasitology, and his numerous awards and honors attest to its importance. He was probably the first to recognize the importance of combining a study of the activities of the parasite with a study of the host's responses. This effort led him inevitably into the study of immunology per se. Tolly's careful, thorough, and precise analysis of the hemolysin response along with his earlier emphasis on the cellular nature of immunity played a key role in redirecting immunology into the mainstream of biology. This pioneering advance has never been adequately acknowledged. Perhaps Tolly's unique ability to work closely with numerous collaborators and his generosity in giving others credit for various phases of the work disguised his contributions. In any case, he

seemed to be ruled by a kind, considerate unselfishness and enlivened and brightened any group with his sparkling ready wit, timely joke, and sunny smile. He derived a mischievous delight in telling his classes of medical students that he was a typical parasite in that *he* always derived benefit and took advantage of the work of others. Above all was Tolly's interest in science. He was a pathfinder in formulating hypotheses of how nature works and in devising methods aimed at solving the questions that arose. I know that for myself the development of the concept of cell-selection arose during almost weekly lunches with him during the period from 1952 through 1957. I also know that the invitation and encouragement to write the associated concept of "Immunological Specificity" for *Science* in 1959 came from this same source. How many other graduate students and collaborators owe a similar debt may never be known.

In conclusion, I would like to append to this biography a poem my wife and I wrote at the time of Tolly's retirement from the University of Chicago in 1960 because it expresses, in a clumsy way, the admiration and deep affection we had for him.

Lines Composed in a High Fever and at a Low Oxygen Saturation
(With apologies to Samuel T. Coleridge)

For Talifer did mother naitch,
A scientific dome decree,
Where comp and hemolysin ran,
Through test tubes numberless to man,
To set a tracer free.

So thrice four sets of complement
Compared with one to battle went;

And here were racks of shiny copper plate
Where stood a thousand test tubes in a row,
And here was Lucy, ever working mate
Directing and helping to plan the show.

But oh! that deep scientific dome which granted
The ideas which shaped the plan
A magic place! both holy and enchanted
Filled with stories ne'er decanted,
Nor would pass a censor's ban.

It is a miracle of rare device
A scientific dome with humor nice.
Could we revive within us
The magic of his song
To such a deep delight 'twould win us
That with music loud and long
We would build his life in verse.

Alas! We are not poets.

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