Jesse Rabinowitz

BIOGRAPHICAL

A Biographical Memoir by Charles E. Samuel

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JESSE CHARLES RABINOWITZ

April 28, 1925—September 9, 2003 Elected to the NAS, 1981

Jesse C. Rabinowitz was a biochemist who made pioneering contributions to the understanding of folic acid coenzymes and iron-sulfur proteins. His work, which employed Clostridia and other Gram-positive bacteria, addressed fundamental problems of microbial physiology and biochemistry, with discoveries that improved understanding of human health and disease processes. Jesse Rabinowitz was also a fine teacher, a humanist, and a devotee of the arts, music, and literature.

Early years and education

Jesse Rabinowitz was born on April 28, 1925, in New York City, the only child of Julius R. and Frances Rabinowitz, Yiddish-speaking immigrants from Eastern Europe. His father, from Russia, was a needle worker in the garment industry; his mother, from Poland, was a homemaker.



esse received his initial schooling in public schools in the Bronx. Then, when he was 11 years old, Jesse moved with his parents to the Roosevelt-Jersey Homesteads project in central New Jersey. The settlement, which had been founded with federal funding during the Depression as part of the New Deal initiative, was an experimental project in communal living that involved about two hundred unemployed Jewish garment workers, who were mostly from the Lower East Side of New York City. They farmed during the summer producing subsistence products, and during the winter they worked in the garment industry.

Jesse studied Yiddish in a Sholom Aleichem School and was in the first class to be graduated from the grammar school in Roosevelt. He went on to earn his bachelor of science degree in chemistry in 1945 from the Polytechnic Institute in Brooklyn, New York. As an undergraduate, he was an excellent student in the sciences and math, as well as in literature, but less so in economics and physical education. His undergraduate dissertation

His contributions to our knowledge were made in multiple areas of biochemistry and microbial physiology, including folic acid coenzymes and one carbon metabolism; ironsulfur proteins, specifically bacterial ferredoxins; purine degradation; and protein biosynthesis, mostly in Gram-positive microorganisms. dealt with phosphorus-containing compounds of the milkweed seed. Jesse then attended graduate school at the University of Wisconsin, Madison, where he earned graduate degrees in biochemistry, a master's degree in 1947 and PhD in 1949, for studies carried out with Esmond E. Snell in the Department of Biochemistry, College of Agriculture, on the chemistry and biology of vitamin B6.

Jesse remained in Madison for one additional year as a US Public Health Service postdoctoral fellow working with David Green in enzymology, before continuing his training in 1951 and 1952 as a US Public Health Service fellow with Horace A. Barker in the Department of Plant Biochemistry at the University of California, Berkeley,

where he studied purine fermentation using *Clostridia*, a bacteria that he would continue studying throughout his career.

He moved to the National Institute of Arthritis and Metabolic Diseases at the National Institutes of Health, in Bethesda, Maryland, as a chemist and biochemist from 1952 until 1957. Jesse then returned to Berkeley in 1957 as an associate professor in the Department of Biochemistry, and he became a lifelong faculty member of the University of California. He was promoted to professor in 1963, served as department chair from 1978 until 1983, and became emeritus professor in 1991. Jesse also held a joint appointment in the Agricultural Experiment Station during his academic career at UC Berkeley.

Scientific interests

Jesse's scientific career was characterized by an ability to identify novel and significant questions and then to gain fundamental insights toward answering them. His contributions to our knowledge were made in multiple areas of biochemistry and microbial physiology, including folic acid coenzymes and one carbon metabolism; iron-sulfur proteins, specifically bacterial ferredoxins; purine degradation; and protein biosynthesis, mostly in Gram-positive microorganisms. Jesse's research was supported by the continuously awarded Research Grant AM-2109 from the National Institute of Arthritis

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and Metabolic Diseases, as well as by the California Agriculture Experiment Station. In recognition of his seminal scholarly contributions, Jesse was elected as a member of the National Academy of Sciences of the United States in 1981 and as a fellow of the American Academy of Microbiology in 1997.

Jesse's interest in microbial metabolism began as a graduate student with Esmond Snell at the University of Wisconsin, where he studied the vitamin B6 group. Among his accomplishments at Madison were the discovery of pyridoxamine phosphate and the use of differential microbiological assays for the determination of different forms of vitamin B6—pyridoxal, pyridoxamine, and pyridoxine—in natural products (Rabinowitz and Snell 1948). As part of his detailed analysis of the use of *Streptococcus faecalis* for the determination of pyridoxamine and pyridoxal, Jesse showed that *S. faecalis* could also be used in the assay of folic acid (Rabinowitz and Snell 1947), a vitamin that became a focus of Jesse's research extending throughout his career on tetrahydrofolate-mediated one-carbon reactions.

Jesse's interest in *Clostridia* and one-carbon metabolism began as a postdoctoral fellow with Horace Barker at UC Berkeley. Barker had isolated two anaerobic bacteria, *Clostridium cylindrosporum* and *Clostridium acidiurici*, which were capable of fermenting purines. Working with Barker, Jesse identified formic acid as a product of fermentation of guanine by *C. cylindrosporum*. He carried out isotope tracer experiments to determine the purine carbon sources of the formic acid, as well as carbon dioxide, glycine, and acetic acid formed by *C. cylindrosporum*. Formic acid was found to be derived chiefly from C-8, and the methylene of glycine from C-5, the carboxyl of glycine from C-4, and the amino group from N-7 (Rabinowitz and Barker 1956). Jesse then continued his studies of purine fermentation independently after his move to NIH, identifying intermediate compounds formed during purine degradation by *Clostridia* and characterizing the enzymatic activities involved in the processes (Rabinowitz and Pricer 1956a). In humans, a final product of purine degradation is uric acid, which is excreted in the urine but can cause the disease known as gout, which is characterized by elevated levels in serum and painful arthritic joint inflammation.

Folic acid coenzymes and one-carbon Metabolism

Many important one-carbon transfer reactions are mediated by the tetrahydrofolate (THF) coenzyme form of folic acid. THF is required for the biosynthesis of purines,

thymidylate, histidine, methionine, and pantothenate, as well as of formylmethionyl-tRNA, which is utilized by some microorganisms to initiate protein synthesis.

Jesse's early studies on purine metabolism in *Clostridia* led to the characterization of three enzymes that catalyze the formation and interconversion of one-carbon derivatives of tetrahydrofolate coenzymes at different oxidation states: formyl tetrahydrofolate synthetase (EC 6.3.4.3) that catalyzes the formation of 10-formyl-THF from THF using formate and ATP; methenyl tetrahydrofolate cyclohydrolase (EC 3.5.4.9) that catalyzes the formation of 5,10-methenyl-THF from 10-formyl-THF; and methylene tetrahydrofolate dehydrogenase (EC1.5.1.5) that, with NADPH, catalyzes the formation of 5,10-methenyl-THF from 5,10-methenyl-THF (Rabinowitz and Pricer 1962; Himes and Rabinowitz 1962; Uyeda and Rabinowitz 1967).

Jesse showed that THF was a cofactor in the metabolism of formiminoglycine in extracts prepared from *C. acidi-urici* and *C. cylindrosporum*, leading to the formation of 10-formyl THF (Rabinowitz and Pricer 1956b). He then established that three enzymatic steps were involved, with 5-formimino-THF and 5,10-methenyl-THF as intermediates in the formation of 10-formyl-THF during reactions catalyzed by formiminoglycine formimino-transferase, 5-formimino-THF cyclodeaminase, and 5,10-methenyl-THF cyclohydrolase (Rabinowitz and Pricer 1956c). A role of folic acid in the metabolism of formimino compounds was also suggested from studies by Herbert Tabor and others, due to the accumulation of formiminoglutamic acid, a histidine metabolite, in the urine of folate-deficient rats. The same intermediates and enzymatic steps were found to occur in the metabolism of formiminoglutamic acid, leading to the formation of 10-formyl THF in extracts of rabbit liver (Tabor and Rabinowitz 1956).

Formyltetrahydrofolate synthetase was a subject of Jesse's research, initially focusing on the enzyme from *Clostridia* strains and then subsequently the enzyme characterized from eukaryotic sources. The isolation and crystallization of the *Clostridial* synthetase (Rabinowitz and Pricer 1962) was followed by characterization of the bacterial enzyme and the enzymatic reaction, work that was carried out by Jesse's first graduate student at Berkeley, Richard Himes (Himes and Rabinowitz 1962). The reaction catalyzed by the synthetase is as follows:

ATP + tetrahydrofolate + formate = 10-formyltetrahydrofolate + ADP + Pi.

The *Clostridial* synthetase was found to be a tetramer composed of four identical subunits with relative molecular mass (Mr) of approximately 60,000 that undergo cation-

dependent association. The synthetase was shown to be specific for formate and the activity dependent upon monovalent cations, with ammonium most effective and sodium least effective as an activator. The isolation of (l)-5,10-methenlytetrahydropteroyltriglutamate from *Clostridia* permitted the preparation of radioactively labeled folates including (l)-[6,7-3H2]tetrahydropteroyltriglutamate, which was then used to study the properties of folate binding by formyl-THF synthetase. Bacterial formyl-THF synthetase bound the triglutamyl coenzymes with an approximately one hundred-fold greater affinity than pteroylmonoglutamyl folate compounds (Curthoys and Rabinowitz 1972).

In contrast with the findings in *Clostridia*, where the formyl-THF synthetase, methenyl-THF cyclohydrolase, and methylene-THF dehydrogenase activities reside in separate proteins, Jesse's lab found that a single protein of Mr=218,00 purified from sheep liver possessed all three THF enzymatic activities: synthetase, cyclohydrolase, and dehydrogenase. The purified protein that displayed the multiple catalytic activities was composed of two identical subunits and was named formyl-methenyl-methylene tetrahydrofolate synthase (combined) (Paukert, D'Ari-Straus, and Rabinowitz 1976). Jesse then turned to yeast and the power of genetics to unequivocally establish that a single multifunctional protein designated C1-THF synthase catalyzes the three THF interconversions in Saccharomyces cerevisiae. The ADE3 gene that encodes the cytoplasmic C1-THF synthase, when overexpressed in transformed cells, produced a trifunctional enzyme identical to the C1-THF synthase purified from wild-type cells (Staben and Rabinowitz 1986). In yeast, C1-THF synthase was also found in mitochondria; however, deletion of the MIS1 gene encoding the mitochondrial C1-THF synthase, interestingly, did not affect cell growth (Shannon and Rabinowitz 1988). The conceptual understanding provided by Jesse's pioneering work on the enzymology of THF interconversions is of immense practical importance. The extensive use of antifolate agents in cancer chemotherapy further fueled interest in enzymes that use folate coenzymes and the structural and functional properties of their folate-binding sites, as well as their sensitivity to inhibitors.

Clostridial ferredoxins

Ferredoxins are non-heme iron electron-transfer proteins (Malkin and Rabinowitz 1967). Jesse's longstanding interest in purine fermentation and the metabolism of pyruvate by *C. acidi-urici* and *C. cylindrosporum*, coupled with the findings of Mortenson, Valentine, and Carnahan about a non-heme iron-containing protein from *C. pasteurianum* required for the formation of acetyl phosphate and hydrogen from pyruvate, led Jesse to examine these *Clostridial* organisms and additional bacteria for ferredoxin.

Relatively large amounts of ferredoxin were found in four different *Clostridial* strains tested (Buchanan, Lovenberg, and Rabinowitz 1963). Furthermore, ferredoxin presence was demonstrated in obligately anaerobic bacteria, but not in aerobic or facultatively anaerobic organisms. The ferredoxins from *C. acidi-urici* and *C. pasteurianum* were purified, crystallized, and characterized.

A series of comparative studies carried out on the two proteins revealed that they were similar, even though the two bacterial strains have different catabolic pathways. The ferre-doxins stimulated acetyl phosphate formation from pyruvate, and both were shown to possess approximately equivalent and high amounts of iron, as well as loosely bound labile sulfide. Both proteins also lacked the amino acids histidine, tryptophan, methionine, and leucine. Subsequent studies were then carried out on the chemical nature of *Clostridial* ferredoxin purified and crystallized from *C. cylindrosporum, C. butyricum,* and *C. tetano-morphum,* in addition to *C. acidi-urici* and *C. pasteurianum.* These *Clostridial* ferredoxins, likewise, were shown to contain similar amounts of iron and inorganic sulfide, with most of the iron as ferrous iron, and to have similar molecular weights of approximately 6,000. Studies on the incorporation of ⁵⁹Fe and ³⁵S-sulfide into ferredoxin, together with analyses using sulfhydryl reagents, indicated that the iron and the cysteine of native ferredoxin were linked covalently (Lovenberg, Buchanan, and Rabinowitz 1963).

Characteristic of Jesse's approach to science, multiple independent methods were typically utilized to answer questions; for example, the determination of the molar extinction coefficient of *Clostridal fe*rredoxin and the iron and sulfide content of the protein. The extinction coefficients obtained by dry weight determination, amino acid analysis, and amino acid release by carboxypeptidase A treatment were in good agreement with each other, and for *C. acidi-urici* ferredoxin at 390nm, the extinction coefficient was 30,600. *Clostridial* ferredoxin was established to contain 8 moles of both iron and sulfide per mole of protein (Hong and Rabinowitz 1970). Purification schemes established by Jesse's lab from the purine-fermenting *Clostridial* were designed to obtain not only the synthetase and ferredoxin proteins, but also pteroyltriglutamate coenzymes. Pyruvate-ferredoxin oxidoreductase was also purified and *Clostridial* ferredoxin was found to transfer two electrons in the pyruvate-ferredoxin oxidoreductase reaction in the presence of excess pyruvate and CoA and a limiting concentration of ferredoxin (Uyeda and Rabinowitz 1971).

Ferredoxin and 10-formyl-THF synthetase were two main focuses during Jesse's research career at UC Berkeley. He was generous in supplying materials and reagents to many investigators, including samples of purified ferredoxin and synthetase, and the bacterial

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strains from which the proteins were purified, including *C. cylindrosporum*, *C. acidi-urici*, and *C. pasteuranum*.

Protein biosynthesis

A third area to which Jesse contributed important insight and understanding is that of the initiation of protein synthesis, predominantly from his studies of Gram-positive bacterial systems. Jesse's lifelong interests in the biochemistry of folic acid and microbial physiology positioned him to recognize novel questions in the area of translation. For example, the initiation of protein biosynthesis was believed to require formylation of the initiator methionyl-tRNA both in bacteria and eukaryotic organelles. This transformylation reaction of met-tRNAi utilizes 10-formyl-THF as the formyl donor. From Jesse's studies as a graduate student with Snell at Wisconsin, he knew that S. faecalis, a Grampositive facultative anaerobe, was not capable of synthesizing folic acid. The vitamin was required for growth, but serine, methionine, thymine, a purine base, and pantothenate could replace the folate requirement. Under folate-deficient conditions, growth of S. faecalis is resistant to the folate antagonists trimethoprim and aminopterin, formylmethionyl-tRNA is not synthesized, and the initiation of the protein synthesis occurs with methionyl-tRNAi that is not formylated (Samuel, D'Ari, and Rabinowitz 1970). Furthermore, when grown in the absence of folate, the initiator tRNA differs in a single position: uracil is found in place of ribothymine in the GTYC loop IV. Also, 5,10-methylene-THF, rather than S-adenosylmethionine, was established as the methyl donor in this RNA methylation reaction to form ribothymidine in S. faecalis, as well as Bacillus subtilus (Delk, Romeo, Nagle, and Rabinowitz 1976).

Jesse strived to define the roles that the ribosomal system and initiation factors played in determining the specificity of natural mRNA recognition and translation in Gram-positive *Clostridial, Bacillus*, and *Staphylococcus* systems, compared with Gram-negative bacteria such as *Escherichia coli*. By testing heterologous combinations of ribosomes and factors from C. pasteurianum and *E. coli* with different mRNAs, it was found that the ribosomes controlled the specificity of translation and that the initiation factors controlled the efficiency dependent upon the mRNA (Stallcup and Rabinowitz 1973). The ribosome-binding site region of the Gram-positive *S. aureus* β -lactamase gene was determined and shown to possess unique features not observed for most of the initiation sites recognized by *E. coli* ribosomes: a novel initiation codon, UUG, initiated translation with methionine; and, a strong Shine-Dalgarno complementarity containing five G-C base pairs preceded the UUG initiation codon (McLaughlin, Murray, Rabinowitz 1981).

A series of synthetic ribosome-binding sites were used to compare, in a systematic manner, the influence of spacing between the Shine-Dalgarno sequence and the initiation codon; the activity of the three different initiation codons (AUG, GUG, UUG) as a function of Shine-Dalgarno strength; and, the effect of secondary structure within the ribosome-binding site on translational efficiency in *B. subtilis* as compared to *E. coli* in vivo. Significant differences were found between the two organisms (Vellanoweth and Rabinowitz 1992). Molecular clones of the *C. pasteurianum* ferredoxin gene were obtained, which led to the mapping in vivo and in vitro of ferredoxin gene transcripts that provided insights from comparative studies of *C. pasteurianum*, *B. subtilis*, and *E. coli* for the promoter elements utilized in Gram-positive organisms (Graves and Rabinowitz 1986).

Finally, during his years as a Professor at UC Berkeley, Jesse enjoyed four sabbatical leaves abroad, all in France. Jesse was a Special Fellow of the US Public Health Service during 1962 and 1963 at the Laboratoire d' Enyzmologie, CNRS, in Gif-sur-Yvette, France, working with J. Szulmajster and B. Nisman. During 1970 and 1971 he was a National Science Foundation Senior Fellow, during 1977 and 1978 a Guggenheim Fellow, and during 1984 and 1985 a visiting scholar, all at the Institut de Biologie Physico-chimique in Paris, working with M. Grunberg-Manago on bacterial protein biosynthesis.

Following Jesse's retirement in 1991, he continued his NIH-funded research for three additional years to bring his pioneering and lifelong studies to a logical stopping point. During his final years at UC Berkeley, to make space more available for new faculty recruitment, Jesse shared laboratory and office space in Barker Hall with Clinton Ballou, also a member of the National Academy of Sciences and a professor emeritus.

Other academic activities

Teaching and Mentorship

Jesse Rabinowitz was highly regarded as a teacher and mentor. For many years, he taught an advanced biochemical laboratory methods course (Biochem 201) taken by the first-year graduate students in the Biochemistry Department. Students learned many things in the "grad lab," which was located on the first floor of what is now Barker Hall. They learned practical techniques in enzymology from Jesse in an era prior to kits and the "kit-generation," techniques that would serve them well during their thesis research and subsequent independent careers as biochemists. Most important, though, was that in

addition to specific biochemical techniques, the first-year graduate students learned the importance of controls and how to critically evaluate data.

Jesse was a superb mentor to the graduate students and postdoctoral fellows that trained in his lab. He had an enthusiasm for science and conveyed to his lab members that scientific research is fun, and that there is a proper way to do science. He provided guidance while allowing his students and fellows to work independently. Trainees quickly learned the importance of proper controls, of reproducibility of datasets, and they learned how to think in a critical manner. Most of the trainees experienced the "we'll see" response from Jesse during a research discussion or lab meeting or literature seminar, his polite way of saying that further in-depth analyses and additional controls were necessary to properly justify a particular conclusion in a convincing manner.

Jesse also had an appreciation for a well-organized laboratory, for meticulous records and lab notes, for orderly lab benches, and for the latest gadgets to facilitate performance of research. The lab environment created by Jesse was congenial and supportive, which was conducive to doing good science. And, in addition to the science, there was an enjoyable social aspect of the Rabinowitz Lab that typically centered around food: lab picnics at Tilden Park or the wine country, lunches or dinner together at a Solano Avenue restaurant, or dinner at Jesse's home, prepared by Jesse or lab members or both working together. As a member of the Rabinowitz Lab, training with Jesse included not only development as a scientist, but also introduction to delicious and interesting cuisine.

University Service

Jesse served on various committees during the 1960s and 1970s at UC Berkeley, both for the Biochemistry Department, illustrated by the Academic Planning Committee to guide the Department, and for the campus, illustrated by the College of Natural Resources Dean Search Committee and the Chancellor's Time and Effort Study Committee. Following his sabbatical in Paris in 1977 and 1978, Jesse, upon his return to UC Berkeley, assumed the chairmanship of the Biochemistry Department and served as the chair for five years, until 1983. Jesse felt that the most valuable resource at the university was its people, and he devoted considerable effort to further enhancing the Biochemistry Department, both as a member of the faculty and when serving chair. Following a period of spectacular hires, he commented, "I think we really have an unexcelled department...."

Professional Service

Jesse was a member of the American Society of Biological Chemists (renamed as the American Society for Biochemistry and Molecular Biology in 1987), which he joined in 1954 and served generously in various capacities, including as a member of the Membership Committee (1968 to 1970) and the Publications Committee (1977 to 1980). He also served two terms as a member of the Editorial Board of the Society's journal, *The Journal of Biological Chemistry*, from 1965 to 1969 and from 1974 to 1978.

Jesse served on the International Union of Biochemistry (IUPAC-IUB) Commission on Biochemical Nomenclature, both on the nomenclature committee for iron-sulfur proteins and as chair of the committee for folic acid nomenclature. On the issue of abbreviations, Jesse felt strongly that they should be based on verbal expression of the substance to the extent possible, so that they would be easily understood. This is exemplified by tetrahydrofolate, which Jesse felt should be designated THF instead of H4-folate.

Jesse and joie de vivre

Jesse Rabinowitz enjoyed a lifelong interest in the arts and humanities, in addition to his scientific pursuits. He was a prize-winning photographer, a superb chef, an accomplished musician, and a serious student of Yiddish and French. Jesse had a passion for travel and considered France his second home to Berkeley. At one point during the 1970s, when he was approached to gauge his possible interest in the chairmanship of a biochemistry department at a leading institution on the East Coast, Jesse replied "…life in Berkeley is…too agreeable to give up voluntarily." Jesse very much enjoyed the culture and arts of the San Francisco Bay area, as well as those of France.

Photography

Jesse was a talented photographer. He received his first camera as a thirteen-year-old, when he was living on the Roosevelt-Jersey Homestead. Photography was to become one of his lifelong hobbies, and during later years he exhibited his work at galleries in the San Francisco area. His subject matter was not so much landscapes, but rather, he photographed people, typically during his worldwide travels.

Jesse's photographs captured the emotions of his subjects' faces in the context of their different cultures. This is exemplified by a collection of photographs published in 2003: *Jesse Rabinowitz, A personal View,* by Peleus Books. Among the photos taken by Jesse is one, on page 55 of the collection, of a child taken in Kabah, Yucatan, Mexico. For this photo, Jesse received the Saturday Review magazine World Travel Photography Grand

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Prize in Color in 1969. In a letter to a friend following retirement, Jesse wrote, "My major effort in time and emotional input is in photography. It is also my chief source of pleasure." Jesse left his extensive collection of photographs to the Special Collections Library at UC Santa Cruz.

Literature

Jesse was a serious student of Yiddish, taking advanced Yiddish classes, and he was a member of a Yiddish reading group in Berkeley. In later years, he stayed in touch with Yiddish events and issues through his computer connection to Mendele, the online Yiddish bulletin board. Jesse was fluent in French, which enabled him not only to present seminars in French, but also to fully enjoy the culture of France during his sabbatical leaves.

Music

Jesse had a passion for music, both as a patron and as a performer. He was a devoted cellist and very much enjoyed the opera. He was a season ticket holder at the San Francisco Opera for more than forty years, beginning from the time shortly after he moved from Bethesda and joined the UC Berkeley faculty. Jesse played cello in chamber music groups in the Bay Area, and he was an active participant in summer music camps, both at home in California and abroad in Europe. In addition to his cello, Jesse made room in his home for a baby grand piano and a harpsichord, which he had purchased at Passau during his first sabbatical to France for use during Chamber music sessions with friends. It was during his 1978 sabbatical in Paris that he purchased a "new" cello, manufactured sometime during the early 1900's, as his cello in Berkeley was undergoing repair while he was away.

Jesse acquired an extensive collection of record albums and CDs of classical and contemporary music over his lifetime. Of these, he generously left a collection of approximately 2,700 classical CDs to the University Library at UC Santa Cruz.

Food and Wine

Jesse traveled while in France, searching for the finest cuisine. At one point, according to a friend, Jesse had dined at every three star restaurant in the country. He also managed time to take cooking courses while living in Paris, and he wrote that he acquired "courage to cook without the book right in front of me, and to forget about exact measurements in most things." However, the chef "does measure for sauces and pates," he added.

Jesse enjoyed exchanging recipes with friends and colleagues for those especially tasty dishes that captured his interest. He had an impressive wine collection in his home cellar,

and his knowledge of wines was superb. Dinner parties at 321 Vassar, Jesse's home, were special whether they were for a seminar guest, a graduating student, or an opera visitor.

Travel

Jesse greatly enjoyed travel throughout his life, both professionally and for pleasure. Canal trips in Europe were among his favorites. During his second sabbatical, in 1970, he took Canal Trip I, which would be the first of ten canal trips in France over the next fifteen years or so. His third sabbatical in 1977 included Canal Trip VII (Canal du Midi), the fourth sabbatical included Canal Trip IX in 1984, and Canal Trip X in 1985 (Canal due Soane).

Even while Jesse enjoyed travel, science was always in his thoughts. During one of his sabbatical leaves to Paris, he had written in the context of a vacation to Denmark to visit friends, "I probably don't deserve a vacation in terms of the way the experiments have

been going, but I can't very well pass up the opportunity," and then, "I had a very pleasant holiday with my friends in Denmark. We had very good things from the farm—a goose for Christmas dinner and some partridge that some hunters had shot and gave to my friend." He also had written to a friend, following retirement: "I am really enjoying retirement. I seem to be busier than I ever was...."

Jesse continued his travels and enjoyment of cultures, and while he was relatively intolerant of the heat, he discovered



A holiday card made by Rabinowitz from his old passport photos.

that he needed to travel near the equator during December and January. Among his postretirement travels was a much-enjoyed trip to study the archeology of the Yucatan.



Epilogue

Jesse Rabinowitz died at the age of 78 from melanoma on September 9, 2003, at his home in Kensington, adjacent to Berkeley, California. Jesse was not only an accomplished biochemist, but also a Renaissance man who truly appreciated the culinary arts, photography, music, and literature. Those individuals who trained with him as students and fellows, and those who were his friends and professional colleagues, owe much to Jesse for his friendship and mentorship.

This biography is based in part on The Jesse Rabinowitz papers, 1944–1999, which are collected at The Bancroft Library of the University of California, Berkeley, and a University of California "In Memoriam: Jesse Charles Rabinowitz." Bruce Ames, Giovanna Ferro-Luzzi Ames, and Edward Penhoet are gratefully acknowledged for their review of this memoir and their helpful suggestions, and Linda D'Ari and Stuart Linn are gratefully acknowledged for providing pictures of Jesse.

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