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ELIZABETH S. RUSSELL
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A Biographical Memoir by

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BY JANE E. BARKER AND WILLYS K. SILVERS

ELIZABETH ("TIBBY") BUCKLEY Shull Russell, one of the truly great figures in the field of mammalian developmental genetics, died on May 28, 2001, at her home on Mount Desert Island, Maine, at the age of 88. In a career spanning five decades, spent almost entirely at Jackson Laboratory in Bar Harbor, Russell did pioneering work on pigmentation, blood-forming cells, and germ cells. She also, more than anyone else, championed the importance of employing genetically defined laboratory animals in all branches of biomedical research.

Looking at Tibby's pedigree one could claim she was destined to become an outstanding geneticist. She was born on May 1, 1913, in Ann Arbor, Michigan, the eldest child of Margaret Jeffrey Buckley, a former teacher at Grinnell College with a master's in zoology, and Aaron Franklin Shull, Ph.D., a zoologist and geneticist at the University of Michigan who authored one of the first textbooks on genetics. Her uncle, George H. Shull, also was a prominent geneticist. He pioneered the development of hybrid corn, coining the word "heterosis," and founded the journal *Genetics* in 1916. Her pedigree also included a physicist, another geneticist, a plant physiologist, and a botanical artist, leaving little doubt that

she would have ample exposure to science. At the age of six her first self-imposed project was the identification and cataloguing of all the flowering plants near the family's summer home. Her interest in science also was fostered by one of her teachers at the grammar school associated with the University of Michigan. The students were taught to make hypotheses based on scientific questions the teacher posed, to design methods to test the hypotheses, and to evaluate and report the results.

Tibby matriculated at the University of Michigan when she was 16 and graduated, Phi Beta Kappa and first in her class, with an A.B. in zoology at the height of the depression in 1933. At her father's suggestion she obtained a scholarship to Columbia University, where she received her master's in 1934. At Columbia Tibby became captivated by the infant field of physiological genetics. Strongly influenced by a Sewall Wright paper entitled "Physiological and Evolutionary Theories of Dominance," she decided to pursue her training in genetics with Wright at the University of Chicago, where she was supported by a teaching assistantship. Her doctoral dissertation, like many Wright students at the time, was concerned with a study of genetic effects on guinea pig coat colors. Tibby received her Ph.D. in zoology in 1937 and married fellow Wright doctoral student William L. Russell the same year.

The couple moved to Mount Desert Island and the Roscoe B. Jackson Memorial Laboratory (as it was then called); here Elizabeth came to be known as "Tibby," a nickname originally bestowed on her by her husband to differentiate her from two other Elizabeths at the Laboratory. Unfortunately, because of nepotistic rules typical of the times, only William Russell was hired as a staff member of the laboratory. Nevertheless, Tibby was provided space in his lab as an independent, unpaid investigator to study tumori-

genesis in *Drosophila melanogaster*. Two publications resulted. In the first (1940) the properties of five benign and one "malignant" tumor were compared and found to be similar (i.e., the putative malignant tumor was not really malignant). The second paper (1942) was concerned with the inheritance of these tumors. While conducting these studies, Tibby was supported as an Elizabeth Pemberton Nourse fellow of the American Association of University Women, beginning what was a lifelong association, including local and state leadership positions with this organization.

Despite raising three boys, Richard, John, and James and a girl, Ellen (all born between the years 1940 and 1946, the year she was finally appointed to the Laboratory's staff), Tibby was able to find time during the 1940s to characterize many of the genetically uniform strains maintained at the laboratory for physical attributes and disease susceptibilities. She also was able to complete a monumental histological study, published in four parts (1946, 1948, 1949) on the effect the major coat color mutations of the mouse have on the physical attributes and distribution of pigment granules in the hair. As far as we are aware this analysis represents the first attempt to define each phenotype of the mouse in terms of the actions and interactions of all the participating factors. It also set the stage for virtually all coat-color studies that followed.

In 1947 Tibby's marriage ended in divorce, with William Russell departing for Oak Ridge National Laboratory in Tennessee, where he and his second wife, Liane Brauch Russell, also went on to become renowned geneticists. Throughout her life Tibby maintained a cordial relationship with the "Oak Ridge Russells." Nineteen forty-seven also was the year of the devastating Bar Harbor fire, a fire that largely destroyed the main laboratory building and wiped out all the mice excepting a few in a fireproof section of

the building. Resisting pressure from friends to relocate the laboratory at some major research center, Clarence C. Little, the laboratory's founder and director, with the enthusiastic agreement of the staff, determined to rebuild on the same site. Tibby was chosen to coordinate the retrieval of Jackson Laboratory mice from scientists around the world so that the lost inbred strains could be reestablished.

While this was a long and laborious process, it resulted in huge benefits for the laboratory, as it focused Tibby's attention on animal health and husbandry matters. She realized that even in the normal course of events, as a preventive measure against either another fire or serious epidemic, there was much to be said for having all the inbred strains represented in a completely isolated facility at the Laboratory. Hence, a so-called inbred nucleus was established; a colony from which all the other breeding colonies of mice at the laboratory were no more than a few generations removed. In 1990 this inbred nucleus was moved to a newly constructed building that was appropriately designated the Russell-Dickie Building in honor of Tibby and her colleague, Margaret Dickie.

Tibby also was the first to realize that because the genetic background can greatly influence the expression of pigment genes, especially those associated with white spotting, it was important that any comparison of the effects of these genes, particularly the pleiotropic effects of alleles, be made on the same genetic background. Accordingly, she laboriously transferred all known coat color mutations onto one of the most widely used strains, C57BL/6J. These congenic strains, which have the bonus of being histocompatible, have been widely used.

Of course, most of Tibby's research efforts were involved with investigating the pleiotropic effects of mutations at the so-called dominant spotting or W locus of the mouse.

Although mutations at this locus affect hematopoiesis and gametogenesis, as well as pigmentation, it is not surprising that it was this last affect that attracted her attention. As she tells it, she was in the mouse room when she was shown a new dominant W mutation, which turned out to be W^v (for viable dominant spotting), that had appeared in Little's mouse colony. Because this new mutation had pronounced effects on pigmentation, her specialty, she was offered the opportunity to study it and compare its effects with those of the previously known *W* allele. And so she was "hooked" and on her way! Tibby's first paper on the W-locus appeared in *Genetics* in 1949. The effort was concerned with the relationship between the effects of *W* and W^v substitution on hair pigmentation and on erythrocytes and indicated that there was a very close connection. The pleiotropic effects of W-locus mutations greatly expanded Tibby's approach to the analysis of gene action. It also necessitated that she become a hematologist as well as an expert on gametogenesis. While much of this was accomplished by spending many hours in the library, it was helped enormously by collaborating and learning from established experts in these fields.

Tibby's first analysis of the effects of *W* and W^v on germ cell development appeared in 1954 in the *Journal of Experimental Zoology*. This histological analysis with Jane Coulombre who had been her summer student, demonstrated that the sterility displayed by *W/W*, W^v/W^v and W/W^v genotypes of both sexes was caused by a germ cell defect. In a subsequent paper, published in the *Journal of Embryology and Experimental Morphology* in 1956, Tibby and her colleagues showed that transplantation of 12-16 day post-coitum (dpc) gonads from anemic fetuses to the spleens of histocompatible castrated adults with normal blood parameters did not alter the donor's capacity to produce germ cells.

Clearly, the effect of W-series genes on germ cells was

autonomous and occurred early in development. The question remained, however, whether the germ cell deficiency stemmed from an inability of the so-called germinal epithelium to produce germ cells, as some believed, or a deficiency in proliferation of a small primordial germ cell stock originating extra-gonadally and entering the germinal epithelium. To resolve this issue Tibby, who favored the former view, collaborated with Beatrice Mintz, who favored the latter view. Taking advantage of the discovery that because of their high level of alkaline phosphatase, the germ cells of the mouse could be selectively stained red by an azo dye coupling method to visualize this enzyme, Tibby and Bea applied this histochemical technique to 8-12 dpc embryos derived from either wild-type parents or from fertile carriers of *W* or W^v. They were able to compare the formation, localization, migration, and multiplication of germ cells in putative anemic mice with those in normals. What they found and reported in 1957 in the *Journal of Experimental Zoology* was that the germ cells in putative anemic embryos form at 8 dpc, but fail to proliferate normally, have low viability, and are retarded in their migration from their site of origin into the germinal ridges. Not only did these observations establish when the germ cell defect in *W/W,* W^v/W^v and W/W^v genotypes become evident but they also constituted the first experimental proof of the extra-gonadal origin of the germ cells in the mammalian embryo.

One of us (W.K.S.) was exceedingly fortunate to spend two years in Tibby's laboratory in the early 1950s as a graduate student from the University of Chicago, and during this period we demonstrated that the agouti series of alleles acted via the hair follicle. Although I was in Bar Harbor to do my thesis research, I was supported as Tibby's technician and as such helped maintain her color stocks. In those days and, as far as I am aware, throughout her career Tibby

weaned once a week with her technician and it was while we were weaning that our agouti locus experiments were conceived. Tibby had called my attention to Sheldon Reed's early experiment on the agouti locus allele, black-and-tan (a^t), and although the results of this experiment were erroneously interpreted, it demonstrated that when neonatal skin grafts are made to neonatal mice, host melanoblasts migrate into graft hair follicles. One afternoon while discussing Reed's findings over the weaning table in the mouse room, it occurred to us that one of the color stocks we were setting up new matings from, was made to order for determining the site of action of lethal yellow (A^y) and nonagouti (*a*). Hence, employing Reed's technique of transplanting skin from one newborn mouse to another, we were able to demonstrate that when nonagouti (*a/a*) melanoblasts migrated into genetically yellow (A^y/-) but non-pigmented skin, they produced intensely pigmented yellow hairs; and conversely when yellow (A^y/ -) melanoblasts migrated into genetically nonagouti (*a/a*) but very lightly pigmented skin, intensely pigmented black hairs were produced. These results demonstrated in definitive and spectacular fashion that it is the agouti locus genotype of the receiving hair follicle that determines the kind of melanin synthesized by the pigment cell. Despite the fact that this study was jointly conceived, that it employed a coat color stock Tibby had originated, and that I was her technician, Tibby had to be convinced that her contributions merited coauthoring the 1955 *Journal of Experimental Zoology* paper that reported the results.

With her W mutations Tibby also pioneered the field of transplantation of blood-forming tissue. In a 1956 publication in *Science,* as well as in a 1959 contribution to the *Journal of the National Cancer Institute,* Tibby and her associates reported that syngeneic blood forming tissue, derived from livers of 15.5 dpc normal C57BL/6 embryos, could cure

the anemia and prolong the life of W/W^v adults when given intravenously into recipients that had received 200r whole-body irradiation. In another 1959 paper with Seldon Bernstein, published in the *Proceedings of the Society of Experimental Biology and Medicine*, prior irradiation was shown to be unnecessary (i.e., because the normal implant had a competitive advantage over the indigenous blood-forming tissue of the host, it replaced the indigenous tissue and produced normal numbers of erythrocytes). These efforts not only revealed there are genetically controlled differences in the functioning of blood-forming tissue but also demonstrated that barring histocompatibility complications, at least some kinds of hereditary anemias might be alleviated clinically by implantation of normal blood-forming tissue.

Inasmuch as Tibby's interest in W required she become an expert hematologist, it is hardly surprising that she became interested in other mouse mutations having effects on erythropoiesis, especially in association with white spotting. This was particularly the case with the mutation Steel *(Sl, Sl^d)*, which also affects germ cell multiplication during the migratory phase. In fact, black-eyed white Sl/Sl^d mice are a phenocopy of W/W^v animals. Hence, once Tibby and her colleagues demonstrated that the implantation of normal blood-forming tissue could cure the anemia of W/W^v mice, attention was focused on curing severely anemic Sl/Sl^d animals by implanting highly congenic +/+ marrow cells. However, all attempts failed. Then, in experiments conducted with E. A. McCulloch's laboratory at the University of Toronto, and employing mice that Tibby had generated, it was found that Sl/Sl^d marrow cells were as effective as +/+ cells in "curing" W/W^v anemia. This observation, reported in *Blood* (1965), indicated that whereas the W defect was intrinsic to hematopoietic cells, Steel's defect was in cells of the hemopoietic microenvironment. Seldon's subsequent demonstration that

the anemic condition of *Sl/Sl*^{d} mice could be ameliorated if they were grafted with an intact, histocompatible *W/W*^{v} spleen also was in accord with this interpretation. As a consequence of these observations Tibby, in a review published in *Advances in Genetics* in 1979, suggested that the normal alleles at the W and Steel loci must interact in some manner, perhaps one was an acceptor and the other bound to it, thus activating the cell. This suggestion turned out to be very prophetic as within the next 11 years both genes were cloned and W (*c-kit*) proved to be the receptor for the Steel (stem cell factor, *scf*) ligand. In fact, *c-Kit* is currently recognized as one the few cell surface markers that identify pluripotent hematopoietic stem cells.

Many of Tibby's research activities in the 1960s were concerned with analyzing mouse hemoglobins, and most of these are cited in a 1974 review (with E. C. McFarland) she published in the *Annals of the New York Academy of Science*. Waelsch and Ranney had described strain-dependent electrophoretic differences in adult mouse hemoglobin in 1957 and Tibby realized these differences would be useful as transplantation markers if they were fixed on the same strain background as her anemic mutants. By that time the 12 different mutations she had accumulated with different heritable blood defects had been moved onto the same homogeneous background as W and Steel. The hemoglobin marker that differed was moved onto the normal parental stock. This marker and others that are more ubiquitously expressed proved to be an enormous boon to transplantation biology. One question that had plagued the W transplantation studies was whether the normal donor provided cells or a substance that stimulated normal blood cell production. By employing the hemoglobin marker Tibby and Seldon (1968) were able to confirm that the normal hemato-

poietic cells injected into the W mice not only cured the anemia but also permanently replaced their red blood cells.

In collaboration with summer students and visiting investigators Tibby also characterized the adult hemoglobin pattern and that of an embryonic hemoglobin variant in 115 inbred mouse stocks of diverse genetic origin. The adult and embryonic hemoglobins were tightly linked (1976). She and her colleagues subsequently described structural differences in adult hemoglobins from six mouse inbred strains and mapped these near the albino locus. A second locus that determined the solubility of hemoglobin and encoded alpha globin variability was studied in 40 different inbred strains. These experiments were a heroic effort since variability at the beta globin locus had an independent effect on the solubility of the hemoglobin and often stocks had to be generated where this anomaly was avoided. These globin variants were of tremendous importance in the 1970s when Tibby and Barry Whitney (1980) discovered a spontaneous mutation that proved to be a model for alpha thalassemia. Finally, mention also must be made of Tibby and Marcia Craig's (1964) important demonstration that in mice embryonic hemoglobins are expressed only in the large nucleated red blood cells from the yolk sac while adult hemoglobins are produced in the fetal liver. This was a seminal finding since it supported arguments that differential gene expression is dependent on factors intrinsic to ontogenic stages.

Tibby also discovered the first mouse model for muscular dystrophy, which she published with her summer student as senior author (1955). This was followed by her laboratory's observation (1961) that the genetic background on which the dystrophia muscularis (*dy*) mutation was fixed influenced its penetrance and expressivity. This observation presaged secondary genes that modify disease expression; genes that more recently have become suspect in patients

carrying an identical DNA alteration but showing marked differences in clinical manifestations.

For many years Tibby also was in charge of all the "retired" animals at the Jackson Laboratory. This not only enabled her to establish life-span data for different strains and some of their F1 hybrids but also because many of these animals were routinely autopsied at advanced ages, information regarding strain differences in susceptibilities to a number of diseases, including different kinds of malignancies. Much of this information served as the basis for Tibby's chapter on "Lifespan and Aging Patterns" in the second edition (1966) of the *Biology of the Laboratory Mouse,* an effort that is still widely cited.

We only have considered some of the highlights of Tibby's scientific achievements. Not to be overlooked, however, is her promotion of the use of genetically controlled laboratory animals in biomedical research. Indeed, her efforts in this regard were carried out with the zeal of an evangelist!

Tibby was elected to the National Academy of Sciences in 1972 and in 1974 she was appointed to its Council, where not surprisingly, she was an active participant in the Institute of Laboratory Animal Resources, waging a vigorous battle in support of the preservation of live animal and plant germ plasm. She also was a member of the American Academy of Arts and Sciences and the American Philosophical Society. In 1974 Tibby was vice-president and president-elect and in 1975-76 president of the Genetics Society of America. In her position as president she chaired a committee charged with drafting a position paper on the sensitive issue of race and IQ. Although this necessitated agreement on the meaning and relevance of IQ among her colleagues, who were from disparate disciplines, the final document was supported with almost no dissent. Tibby also served a five-year term as a member of the advisory council

of the National Institute on Aging and subsequently volunteered for their onsite temporal studies of human health. In 1978 she was appointed by the secretary of health, education, and welfare to co-chair a committee assessing the future need for biomedical researchers. Other awards emanating from Tibby's scientific achievements included being a Guggenheim fellow at the California Institute of Technology (1958-59); inclusion among the Ten Outstanding Women of Northern and Eastern Maine (1983); the Women of Achievement Award from Westbrook College (1985); the University of Maine Maryann Hartman Award (1990); election to the Maine Women's Hall of Fame (1991); and honorary degrees from several Maine-based colleges. She also served as a trustee at the University of Maine (1975-83), College of the Atlantic (1977) and Associated Universities, Inc. (1977-83).

Although Tibby was not a dynamic speaker her infectious enthusiasm, along with her wonderful disposition and most important her genuine affection and concern for students, made her the consummate mentor. She loved to teach and was especially effective one-on-one. It is therefore not surprising that from her first summer at the laboratory, when she supervised 12 students, until her retirement 41 years later, numerous summer students, Ph.D. candidates, and postdoctoral fellows were nurtured and supported in their career goals by Tibby. Indeed, if Tibby had one failing, it stemmed from her eagerness to champion the cause of some of the young people who worked in her lab: She sometimes exaggerated their abilities or overlooked some of their weaknesses. Tibby also developed a summer course in mouse genetics that for many years alternated with the Johns Hopkins/Jackson Laboratory human genetics course. After her retirement the two courses fused. Because retirement was mandatory at the age of 65, Tibby became senior staff scientist emeritus in 1978. With papers

and reviews yet to publish, she continued to work several days a week at the laboratory and, although this activity declined with time, still attended weekly genetics seminars at the laboratory through the year 2000.

After retiring, Tibby became even more involved in health and education matters. She served on Governor Brennan's Task Force on Education for Maine in the 1980's. As a trustee of the University of Maine, she argued vehemently for local branches of the University so that Maine-born employees who refused to leave the state when their employers moved away could have alternative and more available educational experiences . She also taught genetics and global ecology at the College of the Atlantic, a school in Bar Harbor whose focus is on human ecology.

Although Tibby rarely expressed her religious views, she was a devout Episcopalian who regularly attended church and sang a rich alto in the choir. In 1982, after participating in a radiation biology workshop in Egypt, she extended her trip to Liberia to represent the Episcopal Diocese of Maine during the Anglicanization of the Liberian Diocese, a sister diocese of Maine. The Episcopal Bishop of Maine was a good friend of Cuttington College in interior Liberia and it was here that Tibby, at the ages of 75 and 77, returned to teach embryology and genetics. She barely escaped during the civil war in l990, catching the last plane out following a harrowing trip with loyal students to the capital, Monrovia. On her return to Maine she had several life threatening bouts with malaria before it was cured.

One of Tibby's most amazing achievements was raising four F_1's as a single parent at a time when society was not geared up for it, and not only doing a superb job, but doing it while achieving notoriety in her professional pursuits. And, at least to those of us who were on the scene, it all seemed to be accomplished so enjoyably and effortlessly.

At a gathering in remembrance of Tibby held at the

Jackson Laboratory shortly after her death, her son Jim's remarks to those of us who were present were so poignant, and reflected so accurately her spirit and personality that we believe some of them merit repeating here. He remarked that "of course the house and everything in it were in constant disarray, but that's just Tibby. What mattered was we felt secure. We had a rich cultural environment. We benefited from her love, warmth, and good humor, and her wonderful knack of openness and tolerance. She led us on adventures, whenever possible taking the whole family with her to scientific meetings. She taught us to swim and to canoe. She was a Cub Scout den mother. We raised vegetables and cats, dogs, guinea pigs and, occasionally, hell." He also noted that Tibby "didn't just tolerate our teenage shenanigans and soul searching, she lent support wherever our interests carried us. And as we became adults, she stayed engaged, sought our intellectual companionship, and continued to set an example in her own inimitable way." In a story that was so "typically Tibby," he told of one of her trips to Liberia when she failed to take sufficient funds or to arrange the means to get more from home. As she later recounted it she didn't realize her money was gone until after she'd bought textbooks and lab gear for the school. When Jim asked her how she had survived, she said, 'Oh, it was okay, I sold my camera.' She sounded like a college kid on a roadtrip who suddenly runs out of cash!"

Especially significant were Jim's remarks about one of his last visits with Tibby. "She was asleep—never unusual even in the old days. I looked at her for awhile, propped up in her special bed; she had lost weight, some of her appetite and a great deal of mobility, and here she was near the end of her long, rich, complicated journey. When I held her hand she woke. I kissed her and said, 'How are you, Mom?' She looked right at me and said, 'How are you?' I think

that almost said it all. Tibby's interest in and concern for others animated every thing she ever did—and she did a lot."

In the 1970s David Gilmore, Tibby's son-in-law, and Jim redesigned and winterized her summer cottage on Echo Lake in Somesville with floor-to-ceiling windows overlooking the water. It was here that Tibby died peacefully of pancreatic cancer, a disease that had claimed her oldest son, Dick, also a developmental biologist, in 1994. Tibby is survived by her three other children and five grandchildren.

In the summer of 1955 Beatrice Mintz and one of us (W.K.S.) wrote new words to the tune of a song from a very successful Kurt Weill musical of the 1940s, "Lady in the Dark." The song was known as "The Saga of Jennie" and accordingly we called our variation "The Saga of Tibby." Every time I sang it, Tibby, who had a wonderful sense of humor, broke out in smiles and she usually insisted on an encore. It therefore seems fitting to close our tribute with "Tibby's song."

Tibby made her mind up when she was three,
To delve into the mystery of pleiotropy,
So she started with *Drosophila* and as you see,
She ended up with W and W^v.

(Chorus)
Poor Russell, O what a tussle, to get at the common cause,
Of anemia, pigmentation and gonial migration,
Without breaking Mendel's laws.

Tibby made her mind up at seventeen,
To switch the poor old germ cells to a nice red spleen,
So she got herself some castrate hosts without any sex,
But their genotype conferred on them the same old hex.

(Chorus)

Tibby made her mind up at twenty- two,
To study blood formation was the thing to do,
So she radioed for isotopes and got glycine,
And revealed the gory story in the scheme of heme.

(Chorus)

Tibby made her mind up at ninety-eight,
To see the light before she'd sight the pearly gate,
The results are still unpublished but they came out fine,
Yes, Tibby solved the problem at ninety-nine.

SELECTED BIBLIOGRAPHY

1940

A comparison of benign and malignant tumors in Drosophila melanogaster. *J. Exp. Zool.* 84:363-85.

1942

The inheritance of tumors in Drosophila melanogaster with special reference to an isogenic strain of St Sr tumor 36a. *Genetics* 27:612-18.

1946

A quantitative histological study of the pigment found in the coat-color mutants of the house mouse. I. Variable attributes of the pigment granules. *Genetics* 31:327-46.

1948

A quantitative histological study of the pigment found in the coat-color mutants of the house mouse. II. Estimates of the total volume of pigment. *Genetics* 33:228-36.

1949

A quantitative histological study of the pigment found in the coat-color mutants of the house mouse. III. Interdependence among the variable granule attributes. *Genetics* 34:133-45.

A quantitative histological study of the pigment found in the coat-color mutants of the house mouse. IV. The nature of the effects of genic substitution in five major allelic series. *Genetics* 34:146-66.

Analysis of pleiotropism of the W-locus in the mouse: Relationship between the effects of *W* and W^v substitution on hair pigmentation and on erythrocytes. *Genetics* 34:708-23.

1954

With J. L. Coulombre. Analysis of the pleiotropism at the W-locus in the mouse: The effect of *W* and W^v substitution upon postnatal development of germ cells. *J. Exp. Zool.* 126:277-95.

1955

With W. K. Silvers. An experimental approach to action of genes at the agouti locus in the mouse. *J. Exp. Zool.* 130:199-220.

With A. M. Michelson and P. J. Harman. Dystrophia muscularis: A hereditary primary myopathy in the house mouse. *Proc. Natl. Acad. Sci. U. S. A.* 41:1079-84.

1956

With L. M. Murray, E. M. Small, and W. K. Silvers. Development of embryonic mouse gonads transferred to the spleen: Effects of transplantation combined with genotypic autonomy. *J. Embryol. Exp. Morphol.* 4:347-57.

With L. J. Smith and F. A. Lawson. Implantation of normal blood-forming tissue in radiated genetically anemic hosts. *Science* 124:1076-77.

1957

With B. Mintz. Gene-induced embryological modifications of primordial germ cells in the mouse. *J. Exp. Zool.* 134:207-37.

1959

With S. E. Bernstein, F. A. Lawson, and P. Smith. Long-continued function of normal blood- forming tissue transplanted into genetically anemic hosts. *J. Natl. Cancer Inst.* 23:557-66.

With S. E. Bernstein. Implantation of normal blood-forming tissue in genetically anemic mice, without x-irradiation of host. *Proc. Soc. Exp. Biol. Med.* 101:769-73.

1961

With R. Loosli, W. K. Silvers, and J. L. Southard. Variability of incidence and clinical manifestation of mouse hereditary muscular dystrophy on heterogeneous genetic backgrounds. *Genetics* 46:291-99.

1964

With M. L. Craig. A developmental change in hemoglobins correlated with an embryonic red cell population in the mouse. *Dev. Biol.* 10:191-201.

1965

With E. A. McCulloch, L. Siminovitch, J. E. Till, and S.E. Bernstein. The cellular basis of the genetically determined hemopoietic defect in anemic mice of genotype *Sl/Sl*^{d}. *Blood* 26:399-410.

1966

Life span and aging patterns. In *Biology of the Laboratory Mouse*, 2nd ed., ed. E. L. Green, pp. 351-72. New York: McGraw-Hill.

1968

With S. E. Bernstein. Proof of whole-cell implant in therapy of *W*-series anemia. *Arch. Biochem. Biophys.* 125:594-97.

1974

With E. C. McFarland. Genetics of mouse hemoglobins. *Ann. N. Y. Acad. Sci.* 241:25-38.

1976

With R. H. Stern and B. A. Taylor. Strain distribution and linkage relationship of a mouse embryonic hemoglobin variant. *Biochem. Genet.* 14:373-81.

1979

Hereditary anemias of the mouse: A review for geneticists. *Adv. Genet.* 20:357-459.

1980

With J. B. Whitney. Linkage of genes for adult alpha-globin and embryonic alpha-globin-like globin chains. *Proc. Natl. Acad. Sci. U. S. A.* 77:1087-90.

1985

A history of mouse genetics. *Ann. Rev. Genet.* 19:1-28.