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THEOPHILUS SHICKEL PAINTER

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A Biographical Memoir by

BENTLEY GLASS

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Biographical Memoir

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BY BENTLEY GLASS

IN THE STELLAR DAYS OF Drosophila genetics during the 1920s and 1930s, only two principal centers of such research existed in the United States. The California Institute of Technology attracted Thomas Hunt Morgan from Columbia University in 1929, and he brought with him his two students, Alfred H. Sturtevant and Calvin B. Bridges, who a decade earlier had contributed to the establishment of the chromosome theory of heredity. The CalTech group also included Theodosius Dobzhansky, Jack Schultz, and a constellation of notable visiting fellows, present for a year or two, such as George Beadle and Curt Stern.

During the same period a second stellar group formed at the University of Texas in Austin. H. J. Muller, one of the original trio of Morgan's graduate students, had created a great stir in genetics with his 1927 discovery that X-rays will induce mutations at frequencies hundreds, even thousands, of times higher than rates of spontaneous mutation. A generous grant from the Rockefeller Foundation made it possible for Muller, joined by J. T. Patterson and T. S. Painter of the Department of Zoology at Austin, to establish a cytogenetical program for exploiting the new discovery. Graduate students were recruited and given fellowships, the earliest of which went to C. P. Oliver, Wilson S. Stone, and the writer of

this memoir. Muller soon found that X-rays produce chromosomal breaks and rearrangements in addition to gene mutations, Oliver worked out the relation of point mutations to radiation dosage, Painter collaborated with Muller in analyzing chromosomal rearrangements, and Patterson explored an exciting new field—mosaic types of mutation produced by X-rays. Bursts of exciting new findings made the rivalry with CalTech as hectic as a close basketball game, and Painter was a central figure in all of it.

EARLY LIFE AND EDUCATION

T. S. Painter was born in Salem, Virginia, the son of Franklin V. N. Painter and Laura T. Shickel Painter. T. S.'s father was an esteemed educator, a professor of modern languages and English literature at Roanoke College. Both parents were very religious, and their son was brought up in an atmosphere of culture and religious faith that marked him deeply. His middle name was that of his mother's family; his given name reflects his parents' Christian orientation. As a boy, T. S. was sickly and obtained most of his elementary and secondary education by home tutoring. He entered Roanoke College in 1904 and graduated with a B.A. degree in 1908. The college was a small one and did not provide a diversity of scientific courses. Painter was attracted to chemistry and physics but had no opportunity to acquaint himself with biology.

Having received a scholarship in chemistry, he entered Yale University as a graduate student in 1908. Here he met Professor L. L. Woodruff of the Biology Department and asked to be permitted to sit in a corner of the laboratory and look at objects under a microscope, which he had never had an opportunity to use before. Professor L. L. Woodruff assigned Painter a microscope and provided him with a hay

infusion full of active bacteria, protozoans, and algae. Painter was fascinated and soon decided that he wanted to change his field from chemistry to biology.

He received an M.A. degree in 1909 and a Ph.D. in 1913, under the direction of the famed authority on spiders Alexander Petrunkevitch. Painter learned the techniques of cytology as practiced at that time and for his thesis explored the process of spermatogenesis in a species of spider. His first scientific publication (1913,1) was a paper on dimorphism in males of the jumping spider, *Maevia vittata*. His second (1914,1) was his thesis research.

Painter then went to Europe for a year of postdoctoral study, partly in the laboratory of Theodor Boveri, in Würzburg, and partly at the famed Marine Zoological Station at Naples. At that time Boveri was among the foremost cytologists in the world. More than a decade earlier he had established, in studies of the fertilization and development of *Ascaris* eggs, that each chromosome controls development individually. Chromosomes, furthermore—although they seem to disappear after the close of each mitotic cell division—have a persistent continuity and reappear in the next mitosis in the same place they occupied before their disappearance. Most surprisingly, they continue to bear whatever aberrant distinctions they might previously have acquired by accident. Boveri was a stout supporter of the chromosome theory of heredity—which he had enunciated independently of W. S. Sutton, a student of E. B. Wilson at Columbia. Later, when I was taking a graduate course with Painter at Austin, it was a matter of astonishment to me that I never heard him reminisce about those exciting times or make any reference to Boveri or to what he learned from him.

The experience at Naples, with its marvels of marine life for a cytologist to explore, seemed to affect Painter more. His next publications dealt with problems of the forces involved

in the cleavage of the fertilized egg into a multiplicity of cells by means of repeated mitotic cell divisions.

Back in the United States from a war-torn Europe, Painter received an appointment as an instructor in zoology at Yale for two years. He was also asked to teach marine invertebrate zoology at the Woods Hole Laboratory in the summers of 1914 and 1915. There he met two persons who were to be exceedingly important in his life. The first, Mary Anna Thomas, was a young student in his course who would later become his devoted wife. The second, John Thomas Patterson, was the young head of the Zoology Department at the University of Texas in Austin. Patterson offered Painter the academic post that brought him to the institution where he would spend the remainder of his life. In his *Biographical Memoir* of J. T. Patterson (1965,1), Painter told of the warm and friendly way in which the two first met while playing baseball with other teachers and researchers at Woods Hole.

Painter's research at this period greatly resembled the type of experimentation on developing invertebrate embryos favored by E. B. Wilson and E. G. Conklin. He first studied the effects of carbon dioxide on the developing eggs of *Ascaris,* the material for which had been obtained at Würzburg. His next study also took its origin from work begun in Europe, this time at Naples, where Painter had discovered spiral asters in developing eggs of sea urchins and become curious about their participation in the process of embryonic cleavage. He investigated the occurrence of monaster eggs, the light they threw on cell mechanics during division, and the influence of narcotics on cell division. Painter demonstrated that eggs may divide in the absence of asters, that a factor derived from the nucleus is required for division, and that the asters presumably play a regulatory role in the distribution of the nuclear factor.

In May 1916, Painter enlisted in the National Guard at

New Haven and became a sergeant of the Headquarters Company of the Tenth Regiment of Field Artillery. Discharged in September 1916, he married Anna Thomas on December 19, 1917. Their children—two boys and two girls—and, eventually, their grandchildren made a warm, closely knit family.

With the advent of World War I in 1917, Painter was commissioned a first lieutenant of the U.S. Army Signal Corps and was sent to Toronto's Imperial Flying School to find out what measures were needed to establish a ground school of aviation in Austin. After the school was established, he served as a member of its academic board and was promoted in 1918 to captain in the U.S. Army Air Service. In April 1919 he retired as a captain of the Reserve Corps.

Though Painter went to Austin in 1916 as an adjunct professor of zoology, military service interrupted his research for several years, and he was not promoted to associate professor until 1921. Four years later, in 1925, he was appointed full professor with membership in the graduate faculty.

Painter was a man of broad interests and cheerful disposition. He often visited his students in the laboratory to exchange ideas, giving them encouragement as well as direction. He taught undergraduate courses in addition to graduate cytology, and—for many years—a popular premedical course in comparative anatomy. He played tennis and golf and loved swimming, fishing, and crabbing. He was also an inveterate hunter, liking nothing more than to take down his rifle to hunt deer or antelope. He was a fine gardener, and his flower displays were a marvel to all visitors. He particularly enjoyed hybridizing irises to produce new patterns of remarkable color. He was an expert with tools and made furniture for his home. In later years he turned to jewelry-making and again developed great skill at producing objects that reflected his fine taste. He took a strong part

in his church's activities and in various clubs. In many ways the antithesis of the stereotypical Texan, he was both reserved and self-controlled.

CHROMOSOME CYTOLOGY AND SEX CHROMOSOMES

Back at the University of Texas after his military service, Painter resumed his cytological studies of spermatogenesis in a common small lizard, *Anolis carolinensis*. But he quickly turned to a new problem: the number of mammalian chromosomes and their morphology, with particular emphasis on the nature of sex determination.

In the zoology laboratories of the Department, embryologist Carl G. Hartmann was engaged in studying the reproduction of the opossum. "There was 'possum meat all over the lab," Painter remarked, a fine opportunity for him to switch from spiders, marine organisms, and lizards to the enticing field of mammalian cytology.

Almost nothing was known about mammalian chromosomes at the time, although it was supposed that mammals must have sex chromosomes corresponding to those of insects and that an XX(female)-XY(male) distinction would exist. It proved quite easy, in fact, to find the sex chromosomes of the opossum, for they were the smallest pair of chromosomes in the cell, and during spermatogenesis they always lay in the center of a ring of the other, larger chromosomes during the metaphase of mitosis. In those days all tissues used for cytological examination were successively fixed, embedded in paraffin, sectioned, and stained. It was of prime importance to get the tissues fresh from dissection into the fixing fluid. Painter invented a sort of multibladed knife by mounting a number of safety razor blades in parallel, close together, which he used to cut up the spermatogenic tubules of the testis immediately after the organ was excised.

Painter demonstrated that the male opossum's sex is de-

termined by a tiny Y-chromosome in place of one of the female's larger X-chromosomes. He showed that in meiosis of the male's spermatocytes prior to formation of spermatozoa, the X and Y chromosomes pair and then segregate, so that each male reproductive cell carries either an X- or a Y-chromosome, but not both. As in insects, then, if all egg cells carry a single X-chromosome and if fertilization by the two sorts of spermatozoa is random, the X-bearing sperm would produce female offspring; the Y-bearing sperm would produce males.

Having thus shown that sex determination in a marsupial mammal corresponds to the process already known from invertebrates, Painter set his sights on placental, or eutherian, mammals, and—through a fortunate circumstance—was able to obtain fresh human testicular tissue. One of his former premedical students was practicing medicine in a state mental institution in Austin where, "for therapeutic reasons," Painter wrote, "they occasionally castrated male individuals." Painter's former student made it possible for him to obtain and preserve, "within thirty seconds or less after the blood supply was cut off, a human testis" (1971,1). We students in the Austin laboratory speculated widely that such tissue was also obtained from criminals executed at the nearby Huntsville prison, but this was probably just idle gossip. Painter himself never confirmed such a source.

Painter's first work on human chromosomes, therefore, preceded his study of primates, though their order of publication was reversed. A year before he published his fuller account of human spermatogenesis and human sex chromosomes (1923,1), a short announcement on the sex chromosomes of "the monkey" appeared in *Science*.

To solve the enigma of sex determination in humans, Painter turned to two species of monkey—the New World Brown Cebus and the Old World Rhesus (*Rhesus macacus*). As

he pointed out in this pioneering work (1924,3), it was highly desirable and perhaps necessary to establish four matters for each species examined: (1) the morphology of the diploid chromosome complex and the chromosome number of the male; (2) the haploid number revealed in the second spermatocytes; (3) the morphology and behavior of the sex chromosomes (X and Y) during meiosis; and (4) the morphology and chromosome number of the female complex. Cross-checks among these observations should bar all possibility of error, even though many species of mammals—including the primates Painter was investigating—have many more and much smaller chromosomes in their karyotypes than do opossums or the insect species in which the chromosomal determination of sex was first established. (A "karyotype" is the term used to designate the entire group of chromosomes characteristic of a cell of a particular species. This could be a diploid cell with two complete sets of chromosomes or, more frequently, the chromosome complement of a haploid cell with a single set of chromosomes—one of each distinctive kind characterizing the species.)

Painter's demonstration of the X-Y type of sex determination in these mammals and in the human species was compelling. His drawings of the larger X-chromosome and the much smaller Y-chromosome, connected to each other by a thin strand while segregating in the first prophase of meiosis, left no doubt.

The number of chromosomes was less certain. Some human cells seemed to show a count of forty-eight chromosomes in the diploid primary spermatocyte, others only forty-six. Previous investigators of human chromosome number also varied in their counts, though most settled for forty-eight.

Painter himself took the evidence of his "best cell" and reported the number as forty-eight, confirming an error that

would be perpetuated in dozens of textbooks (including one of my own) until a new set of techniques for counting chromosomes was introduced in the mid-1950s. In 1956, using new stains (such as acetocarmine and Feulgen's stain specific for DNA) and soft somatic tissues (especially embryonic tissues) that could be smeared; using colchicine to halt dividing cells in metaphase and hence greatly increase the number of such cells observable; and using hypotonic salt solutions to spread the chromosomes of dividing cells apart to eliminate their clumping into uncountable masses, J. H. Tjio and A. Levan made a definitive determination that the human diploid chromosome number is forty-six, i.e., twenty-three pairs of homologous chromosomes in human diploid cells.

Painter experienced deep chagrin over this error in what had long been regarded as a primary discovery for which he was known and universally cited. Yet—given the source of his material and the procedures available to him in the early 1920s—he may not have been entirely wrong. Individuals with mental disorders are not prime material for determining normal chromosome number and morphology, for they sometimes have forty-seven, forty-eight, or even more chromosomes and exhibit more frequently than normal persons translocations and deletions of chromosomes that would appear to alter their number.

Recently T. C. Hsu, a well-known cytogeneticist, reexamined some of the original preparations on which Painter based his erroneous chromosome count and found that the chromosomes were so badly clumped and cut into segments by the microtome knife, it was a marvel Painter was able to find any cells at all that seemed to give a clear chromosome count. Given that human chromosomes are exceedingly small, that the dyes used in the 1920s darkly stained other matter in addition to chromosomes, and that microtome slices rarely produced whole, undamaged cells for examina-

tion, Painter's error was wholly natural and forgivable. In any case, it in no way diminishes the importance of his discovery of the XX-XY mechanism for determining sex in mammals (including humans), a significant contribution to science.

Painter subsequently examined and recorded the chromosome number of the horse (probably 60; XX-XY sex determination), the bat *Nyctinomous mexicanus* (2N = 48), the European hedgehog (2N = 48), the armadillo (2N = 60), the rabbit (2N = 44), and the dog (2N prob. 52). Additional marsupials examined included—besides the opossum (2N = 22)—*Phascolarctus* (2N = 16), *Sarcophilus* (2N = 14), *Dasyurus* (2N = 14), and the kangaroo *Macropus* (2N = 12). Painter identified an XY pair of sex chromosomes in all of these marsupial and placental mammals except the hedgehog, armadillo, and dog—species he did not investigate extensively enough to judge—though an XY male type was not excluded in them either.

In summary, Painter showed that marsupial mammals in general have a lower chromosome number than placental mammals; that all, or almost all, placentals (including humans) have a high chromosome number ranging from forty-four to sixty; and that all of them have, or probably have, an XX-XY type of sex determination depending upon a particular pair of sex chromosomes in which the Y-chromosome (carried by the male) is far smaller in size than the X-chromosome.

If these studies placed Painter in the first rank of cytogeneticists, the focus of his next research project established him firmly in the forefront of classical genetics. One of Painter's students, E. K. Cox, had determined that the chromosome number of the common house mouse, *Mus musculus*, is forty. Yet W. H. Gates reported that a Japanese waltzing mouse found in the F1 offspring of a cross between normal (dominant) and Japanese waltzer (recessive) parents seemed

to owe its phenotype to the loss of the chromosome carrying the normal dominant allele.

Carefully examining descendants of this mouse, Painter found that all of them had the full complement of forty diploid chromosomes. He also determined that the males carried a typical XY chromosome pair and concluded, therefore, that the original mouse found to be exceptional by Gates could not have suffered the nondisjunctional loss of an entire chromosome—the one carrying the normal allele of the waltzing gene. He hypothesized instead that there had been a deletion of the part of that chromosome that normally carries the allele in question—a hypothesis he subsequently verified by observing that these mice carried *two* heteromorphic pairs of chromosomes, the sex chromosome pair, plus another pair in which one homologue was very much smaller than its partner. Painter's study of the Japanese waltzing mouse appears to have been the first cytological identification of a deletion producing a specific genetic effect (1927,1).

DROSOPHILA CYTOGENETICS

"One day," Painter wrote, " . . . I found [H. J.] Muller down on the floor with a pipette trying to recover some ovaries which he had spilled from a dish. As skillful as he was in genetic analysis, he didn't have great skill in handling such small material. So I suggested to him—I think I caught him just at the right time—'Why don't you let me study those ovaries and tell you where the oogonial chromosomes have actually been broken?' Again, it was a case of being in the right place at the right time! Muller furnished me with female Drosophila carrying a translocation and by examining oogonial metaphases I would determine how much of an exchange had taken place." (1971,1, pp. 34–35.)

So began a collaboration that eventually led to groundbreaking, parallel investigations of genetic and cytological

variations induced by the action of X-rays on genes and chromosomes and to Painter and Muller's paper on the parallel cytology and genetics of induced translocations and deletions in Drosophila—a genetics classic (1929,1).

Though translocations investigated (III-Y and III-II) did not at that time reveal the fact that all translocations are actually reciprocal exchanges, they did show that the size of the cytological piece taken from one chromosome and attached to another did not correspond precisely in size to the portion of the genetic map that was translocated. The importance of this observation was greatly enhanced by the finding that—in the case of deletions of a coherent portion of the genetic map of the X-chromosome—the cytological loss was much greater than would be expected from the ratio of the lost portion to the total genetic length of the chromosome. This finding led, furthermore, to the discovery that there is a large portion of "heterochromatin" at the base of the X-chromosome—a segment that appears to carry few, if any, genes. Most of the deletions excised a considerable part of this heterochromatin.

The two authors went on to find a case of a new linkage-group established by the translocation of a fragment carrying certain genes to an independent spindle fiber attachment. Only much later was it learned that this case represented a translocation of a portion of an autosome to the basal portion of a Chromosome IV that—having lost most of the regular fourth chromosome genes—could freely undergo nondisjunction, eventually to become a new pair of chromosomes. Painter published a cytological "map" of the X-chromosome that reflected this discovery, and Muller reported on their joint studies at the Sixth International Congress of Genetics in 1932.

What is generally regarded as Painter's most notable discovery in cytogenetics occurred in 1932, while the writer of

this memoir was still a graduate student in his Department. Quite independently, but simultaneously with E. Heitz and Hans Bauer in Switzerland, Painter identified the strange-looking tangled balls of thick strands to be seen in the nuclei of the salivary glands of all Diptera (first described by E. G. Balbiani in 1881) as being closely paired homologous chromosomes. Aided by the wealth of established genetical information then available on *Drosophila melanogaster*, he then carried the genetic analysis considerably further than his codiscoverers in Europe.

Painter also introduced a new cytological method for making salivary gland preparations, mentioned casually in his first paper announcing the new kind of chromosomes (1933,2). It was an application of the acetocarmine smear method, long used by cytologists who worked on maize chromosomes. Painter adapted the method to the fruitfly. He simply dissected out the salivary glands from a third instar Drosophila larva in a drop of physiological saline solution, transferred the glands to a drop of acetocarmine stain, placed a coverglass over them, and—under the dissecting microscope—pressed with the point of a dissecting needle on each nucleus within the gland. When an appropriate amount of pressure was exerted, the nuclear membrane burst and the released chromosomes took up the stain in their numerous crossbands.

Painter saw that there were six strands, one short and five long. Each strand remained attached at one end to a mass identified as a "chromocenter," the fused heterochromatin of each chromosome. Painter identified each chromosome by using Drosophila stocks that had a deletion of a portion of one chromosome that would enable that particular chromosome to be picked out. One strand was identified as the X-chromosome; two as the respective left and right arms of Chromosome II; and two as the left and right arms of Chro-

mosome III. The short strand, by process of elimination, was Chromosome IV. Painter recognized, again from the study of the giant Drosophila chromosomes in individuals that were heterozygous for a deletion, that each strand consists of two closely-paired, homologous chromosomes.

By using a variety of genetically known stocks containing deletions of short portions of the sequence of genes in the X-chromosome (the supply of which was expertly furnished to Painter by Wilson S. Stone), Painter quickly made a cytological salivary chromosome map of the X-chromosome of *D. melanogaster*. The cytological sequence of genes was in the same order as the known genetic map of X-chromosome loci based on crossover frequencies, but the distances between genetic loci did not correspond exactly to the cytological map. While certain regions were expanded somewhat, others were contracted. In general, however, the agreement was very good—better than for the agreement between crossover linkage maps and the cytological map derived from ordinary somatic or germ cells that did not develop giant chromosomes.

In a second paper published in 1934, Painter continued his analysis of giant salivary gland chromosomes in stocks carrying deletions, inversions, or translocations. When one chromosome of a homologous pair carried a deletion, the longer mate formed a loop or buckle at the region, so that the exact points of breakage of the deletion could be determined at the level of individual crossbands. In the case of a heterozygous inversion, a large loop was formed with the two homologues passing around the loop in opposed directions, so that every band could still find and pair precisely with its mate in the other chromosome. In translocations a cross-shaped figure would result, for at the point of the exchanged strands, the chromosomes would switch partners.

From these studies it became apparent that all translocations are in fact mutual—or reciprocal—exchanges, even

though the fragment from one chromosome may be large and that from the other very small. It also became established, as Muller and others had previously conjectured, that the reattachments of fragments of broken chromosomes take place only between two broken ends, as though they were in some way "sticky," or as we would now say, through the reunion of broken chemical bonds.

These studies showed conclusively, as the genetic studies had intimated, that the attraction between homologous chromosomes is point by point, locus by locus, band by band, and not a synapsis caused in some vague way by chromosomes as entire units. From the standpoint of physics and chemistry, this conclusion is one of the most interesting findings of cytogenetics.

At this stage of his career, honors came rapidly to T. S. Painter. Yale University conferred on him the honorary degree of D.Sc. in 1936. He was awarded the Daniel Giraud Elliot Medal of the National Academy of Sciences in 1933 and was elected a member of the Academy in that same year. He was elected a member of the American Philosophical Society in 1939.

Painter was greatly interested in the nature and function of the heterochromatin. From the comparison of salivary chromosomes with those of regular somatic cells or cells of the germ line, he concluded that about three-eighths of the X-chromosome of Drosophila is missing in the salivary gland chromosomes, and that the Y-chromosome of the male is missing almost entirely, although in the usual somatic cells the Y-chromosome—unlike the Y of a mammal—is very large, almost as large as the X-chromosome. The apparent disappearance in the salivary gland cells of the heterochromatin must, he thought, be related in some way to difference in function. The salivary gland cells did not seem to carry the usual kind of genes that become evident from their mutation.

Musing over this problem, he was led away from the detailed task of chromosome mapping, which he willingly left to Calvin Bridges' sharp eyes and unending appreciation of detail.

Painter resolved to seek out the functions of different kinds of genetic material, especially the heterochromatin. How, he wondered, does the altered nature of chromosomes in particular organs, such as salivary glands, relate to specialized cellular function?

Except for a joint paper with Wilson Stone on the relation of chromosome fusion to speciation in the Drosophilidae (1935,3), and two papers (1935,2 and 4)—one written jointly with J. T. Patterson—on the salivary gland chromosome map of Chromosome III, Painter concentrated on this new direction until his research was interrupted in 1944.

With his student Allen Griffen, he examined the course of development of the salivary gland nucleus in the fly *Simulium virgatum* in order to see just how the giant paired salivary gland chromosomes arose and what their structure might be in comparison with simpler, single-stranded chromatids of more ordinary cells. With another student, Elizabeth Reindorp, he traced the development of endomitosis in the nurse cells of the Drosophila ovary, a process that gives rise to multistranded chromosomes that do not aggregate and consolidate into giant chromosomes of the salivary gland type.

He studied the synthesis of cleavage chromosomes and demonstrated that the rapid series of cleavage divisions, involving the synthesis of great numbers of new chromosomes from the original new sets in the zygote, or fertilized egg, would be impossible were it not for the abundant feeding of amino acids and nucleotides derived from previously synthesized proteins and nucleic acids in the nurse cells into the oocyte during its period of maturation. Cases of cytoplasmic or matroclinous inheritance might also be explained by the

accumulation of such materials in the cytoplasm of the egg cell. Painter summarized this work at a Cold Spring Harbor Symposium in 1940 (1941,2).

With A. N. Taylor he continued working on nucleic acid storage in the toad's egg, while with J. J. Biesele he examined the alterations in the nature of chromosomes in cancerous cells of the mouse, where much endomitosis and polyploidy were found.

Painter even undertook to assay the relation of cell growth in the pollen grains of a flowering plant, *Rhoeo discolor*, to the amounts of nucleic acid they possessed—an investigation he initiated prior to Avery, MacLeod, and McCarty's demonstration that, in pneumococcus transformations of genetic type, it is the nucleic acid, not protein, that acts as the genetic material. In light of this research, Painter also seems to have suspected that nucleic acid was the material responsible for the hereditary transmission of characters.

UNIVERSITY ADMINISTRATION

In 1944 T. S. Painter's professional life changed abruptly: he became a university administrator. The president of the University of Texas at that time had defended the academic freedom of two faculty members who had engaged in liberal political activities and spoken at meetings of labor organizations. The Regents of the University forced the president to resign and looked hastily for a caretaker who could be expected to refrain from political action and at the same time would be of high academic reputation. A committee of three members of the faculty met with the Regents in order to make suggestions for a resolution of the difficulties, and Painter was one of the three. According to the minutes of the Special Committee of the Faculty that was delegated the task of preparing a memorial resolution following Painter's death,

the committee of which Painter was a member met with the Regents and then retired for the night.

After Dr. Painter was asleep, he was called and asked to return to the meeting. He was told that the president had been dismissed. The Board of Regents asked Dr. Painter to become the acting president. He faced a dilemma. His research program was at a critical stage. He received many pro and con opinions from the faculty and other friends of the University. Finally he decided to accept the temporary appointment because that seemed to be the best way to keep faculty control over the destiny of the University of Texas. He and the Regents asked the faculty to form a committee to suggest nominees for permanent president. When no satisfactory nominee was named, the Board of Regents appointed Dr. Painter to be president so that he could have full authority to carry out the needs of the University. The appointment was accepted with the stipulation that the term would last only until a satisfactory president could be found. Twice Dr. Painter wanted to resign from the presidency but each time he was persuaded to continue in the position. In 1952, his resignation was accepted and he returned to his duties as a teacher.

Without a doubt Painter served his university effectively during a most trying period. He played the role of conservative in the best sense. Although some members of the faculty protested when he accepted the change from acting president to president, because they felt that this was a repudiation of his promise not to accept an offer for the full presidency, it may have been the only reasonable solution at the time to an irreconcilable conflict between the state—represented by the Board of Regents and the governor—and the faculty of the University. Today, after decades have passed, the entire academic community can be grateful for Painter's skill at mediation and compromise. He retained the respect of all.

RETURN TO SCIENCE

Perhaps no challenge to a scientist who has absented himself for some years is as great as that of returning to an active program of scientific investigation. The exponential advance

of science necessarily implies that during a lapse of even two or three years from the laboratory, fundamental changes in understanding will have occurred to such an extent that the returned scientist's grasp of current knowledge and mastery of available techniques are outmoded.

So it was with Painter, but his determination was indomitable. His colleagues testify that he spent more time in the library reading current periodicals and books than did any graduate student. He also asked to be reassigned to the teaching of cell biology to undergraduates and cytology to graduate students, and thus added to his burden all the reviewing and relearning required for teaching. As the Memorial Resolution prepared by his fellow faculty members records, he was successful:

> He developed a good knowledge of modern cellular molecular biology. Often he noticed that a researcher's data could be used to answer in part some classical biological problem, although the author had not mentioned that possibility. The interpretations were too narrow in coverage. As a consequence, Dr. Painter decided to teach his students the recent, chemically-oriented discoveries and to make certain that they had a broader basic training in biology so that they could understand the biological implications of the discoveries. To Dr. Painter, a narrow channel of research may find answers for one small field of interest, but it will not serve the purpose of biology unless it has some major impact upon a basic biological problem.

One can verify his concern with the broader implications by glancing at eleven scientific papers written by Painter between 1955 and 1969. They seem to follow naturally from the earlier work on the salivary chromosomes of dipterans and the endomitosis in the nurse cells of the ovary. But they all probe the greater question of how it is that the hereditary materials passed down from one generation to another in the course of reproduction are converted into a multiplicity of end products in different tissues.

Working with J. J. Biesele again—and with the advantage of electron microscopy—Painter was able to show how the

precursors needed for the secretion of royal jelly (the only food consumed by the queen bee) are produced in the honeybee in special gland cells of young worker bees. Producing as many as 1000 eggs a day, the queen bee requires a considerable supply of both proteins and DNA, which is supplied by the royal jelly. When workers feed heavily on bee bread, their gland cells develop and produce the royal jelly.

According to George E. Palade, Keith Porter, and others, royal jelly gland cells in the young worker bees produce the proteins by means of an extensively developed endoplasmic reticulum. Painter and Biesele searched for the origin of this cellular structure of endoplasmic tubules that apparently derive from outpockets of the nuclear membrane of the cell as the gland cell undergoes endomitosis. As this process enters a stage comparable to the prophase of ordinary mitosis, the numerous nuclei in the gland cell fragment and a myriad of ribosome-like bodies pass out through nuclear pores to become the polyribosomes attached to the walls of the endoplasmic tubules. This process clearly shows how an ovum becomes enriched with protein and nucleotides.

In his final paper, Painter advised young researchers from his own experience:

> "I get the impression that young people [today] master some sophisticated technique such as labeling cellular structures with radioactive isotopes followed by autoradiography, DNA and RNA hybridization, ultracentrifugation in gradients and all the rest and then look around to see how they can use their acquired skills! From my experience I think you should first select and define some broad biological problems, select a suitable material upon which to work and use any available techniques for the solution of your problem. The most important thing is for you to have a biological and not a test tube approach." (1971,1)

How well his own research exemplified that ability to identify the problem, find the right material, and develop the necessary techniques!

Although research always stood foremost in his heart, Painter found time and energy for many other activities. He served on the University of Texas Premedical, Predental, and Library committees. He frequently attended the meetings of scientific societies and, in addition to serving on other committees of the American Philosophical Society, was a member of its Council from 1965 to 1967. He served for six years on the Council of the National Academy of Sciences and six more on its Finance Committee. He was a member of the American Society of Zoologists, the Genetics Society of America, the Association of American Anatomists, the American Society of Naturalists, and the Società Italiana di Biologia Sperimentale.

He was a member of the Boy Scouts of America Committee (1935–40), an advisor to the Dental Research Council (1949–52), and advisor on research to the American Cancer Society. He served on the Commission on Colleges and Universities of the Southern Association and was its chairman for three years; the Southern Regional Education Board; the National Committee on Accreditation; and the Board of the Institute of Nuclear Studies at Oak Ridge. He was a National Lecturer for Sigma Xi in 1936–37. Locally, he was a member of the Rotary Club, Town and Gown, and the English Speaking Union.

He was elected to the Hall of Fame for Famous Americans, served as president of the American Society of Zoologists in 1940, and received the first M. D. Anderson Award for Scientific Creativity and Teaching from the M. D. Anderson Hospital and Tumor Institute in 1969. Perhaps what he regarded most highly among his honors was his elevation to the rank of distinguished professor of the University of Texas in 1939.

It was characteristic of him that he died as he had lived—suddenly, on his return home to Fort Stockton, Texas, from

a hunting trip, in his eighty-first year and as active as ever. Two papers—"The Origin of the Nucleic Acid Bases Found in the Royal Jelly of the Honeybee" (1969,1) and "Chromosomes and Genes Viewed from a Perspective of Fifty Years" (1971,1)—appeared posthumously.

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