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JOHN SPANGLER NICHOLAS

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A Biographical Memoir by

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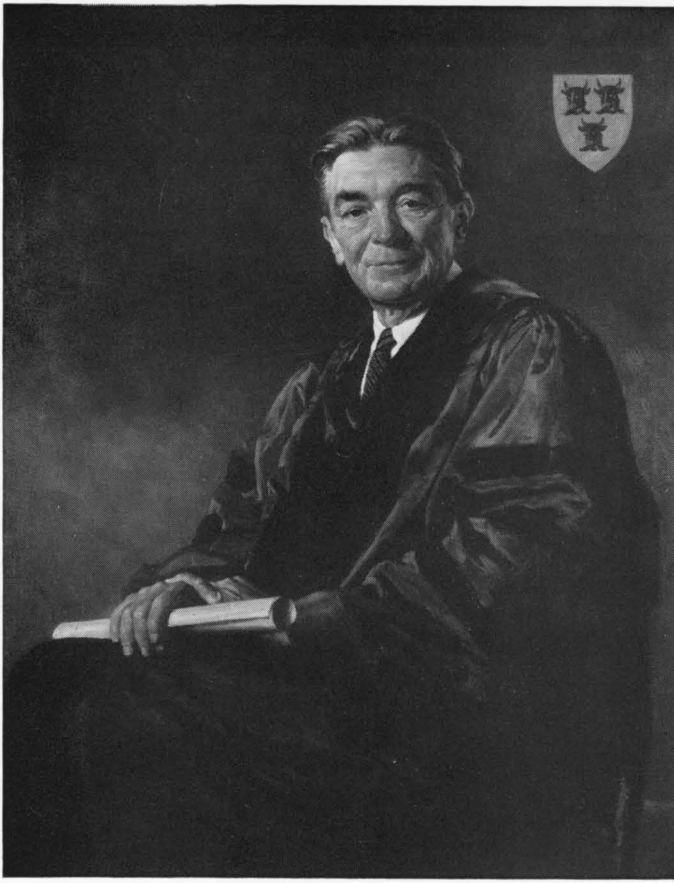

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March 10, 1895–September 11, 1963

BY JANE M. OPPENHEIMER

There is a line among the fragments of the Greek poet Archilochus which says: "The fox knows many things, but the hedgehog knows one big thing." Scholars have differed about the correct interpretation of these dark words, which may mean no more than that the fox, for all his cunning, is defeated by the hedgehog's one defense. But, taken figuratively, the words can be made to yield a sense in which they mark one of the deepest differences which divide writers and thinkers, and, it may be, human beings in general. For there exists a great chasm between those, on one side, who relate everything to a single central vision, one system less or more coherent or articulate, in terms of which they understand, think and feel—a single, universal, organizing principle in terms of which alone all that they are and say has significance—and, on the other side, those who pursue many ends, often unrelated and even contradictory, connected, if at all, only in some *de facto* way, for some psychological or physiological cause, related by no moral or aesthetic principle; these last lead lives, perform acts, and entertain ideas that are centrifugal rather than centripetal, their thought is scattered or diffused, moving on many levels, seizing upon the essence of a vast variety of experiences and objects for what they are in themselves, without, consciously or unconsciously, seeking to fit them into, or exclude them from, any one unchanging, all-embracing, sometimes self-contradictory and incomplete, at times fanatical, unitary inner vision. The first kind of intellectual and artistic personality belongs to the hedgehogs, the second to the foxes; and without insisting on a rigid classification, we may, without too much fear of contradiction, say that, in this sense, Dante belongs to the first category, Shakespeare to the second; Plato, Lucretius, Pascal, Hegel, Dostoevsky, Nietzsche, Ibsen, Proust are, in varying degrees, hedgehogs; Herodotus, Aristotle, Montaigne, Erasmus, Molière, Goethe, Pushkin, Balzac, Joyce are foxes.

Isaiah Berlin, *The Hedgehog and the Fox*.[1]

IT WOULD BE inappropriate in the extreme to compare Nicholas' contributions with those of Goethe, Pushkin, and Balzac; he was simply one of those "human beings in general," to whom Berlin refers in the above quotation, who lead centrifugal lives. But he was extraordinary, too, in his own way. Highly versatile and original, he was endowed with stores of energy, intellectual and physical, that enabled him to make an unusually large and varied number of contributions to biology, both as an investigator and as a teacher. He was productive not only as a scientist; he served Yale in a variety of educational capacities during the greater part of his life, and performed important administrative services for both the University and the government for many years. And his life was many-faceted in other ways also, as we shall see.

Even the most sanguine of molecular biologists (if molecular biologists permit themselves to be described in humoral terms) would not suppose today that the base order in DNA codes accounts directly for attributes of personality. But Nicholas' parents were also both unusually energetic and vigorous, with great drive, powers of organization, and intelligence, and we may assume that one way or another, through heredity or environment, these factors influenced the later professional development of their son. His reasons for becoming a scientist will become apparent later, but meantime let us look more

[1] Cited from *The Hedgehog and the Fox*, by Isaiah Berlin, Simon and Schuster, Inc.; copyright 1953 by Isaiah Berlin.

closely into his life and his background during his early and formative years.

Members of the Nicholas family first came to America as Hessian mercenaries, but abandoned the Loyalist cause to join von Kalb's forces. Our Nicholas' father, the Reverend Samuel Trauger Nicholas, the son of a truck farmer, was born in Kintnersville, Pennsylvania, a few miles south of Easton, still a sleepy but lovely village on the Delaware River and the Delaware Division Canal. He graduated from Pennsylvania (now Gettysburg) College in 1890 and from the Gettysburg Lutheran Theological Seminary in 1893; he was later to become a Doctor of Divinity *honoris causa,* and he advanced far in his profession as a Lutheran minister. Nicholas' mother, née Elizabeth Ellen Spangler, born in Arendtsville, Pennsylvania, was the daughter of the proprietor of the village store. The Spanglers, too, are an old family in Pennsylvania; Spangler's Spring, a landmark on the Gettysburg battlefield, is on land that belonged to Nicholas' maternal grandmother's family. Elizabeth Ellen Spangler completed a teacher's training course at the Shippensburg Normal School. She sang in the church choir at Arendtsville, and it was there that she met the Reverend Samuel Nicholas. They were married in Arendtsville on June 17, 1894, and John Spangler Nicholas, their only child, was born in the Troy Hill section of Allegheny, now part of Pittsburgh, on Sunday, March 10, 1895, between 7 and 8 A.M., in time for an announcement to his father's congregation at the eight o'clock morning service. He was named John for his paternal grandfather, John Nicholas; his parents called him Spangler, but to his friends, at least from his college days onwards, he was Nick.

His parents worked indefatigably in the service of the church, and Elizabeth Nicholas, no less ardent a worker than her husband, was very popular with the parishioners. She devoted herself selflessly to parish duties even when her son was a young child. He was therefore entrusted to the care of Sophia (Mrs. John) Diebold, whom he called Aunt Suff, and this was for him a happy arrangement, as she became almost a second mother to him and he adored her. He once said of her that she was the only person in the world who thought he was always right. To those who knew him later this offers a clue to some aspects of his complicated personality. The approval of his friends and colleagues was always important to him, and even in his laboratory he was an intensely social being.

Nicholas' father was a short man of only five feet four inches; he was one of a large family and called himself "the runt of the litter." He had had a broken leg badly set; his son said that it was in attempting to compensate for what he regarded as his handicaps that he exerted tremendous energy and tenacity in securing the goals he set for himself. Things in life came to him, according to his son, with difficulty and with real effort. The son was later to exert similar energy and tenacity, although things in life were to come easily to him.

Nicholas, the son, was physically well built and extraordinarily well coordinated, a feature that was to stand him in good stead in his chosen profession. His physical resemblance was to his mother; he had her charm and ready friendliness, and presumably he inherited from her his musical talents, of which we shall speak further below.

Both parents were truly interested in their son's intellectual welfare. His father taught him Greek; his mother tutored him at times, and from her, he said later, he learned correct habits of study. Nicholas' parents hoped that their son would enter the Lutheran ministry. But when Nicholas entered college he planned to choose medicine for his profession. This decision resulted in considerable part from the influence of his uncle, Dr. Harry Spangler, a surgeon who practiced in

Carlisle, Pennsylvania. Nicholas described later the vivid impressions made on him, when he visited Carlisle as a young child, by the experiences of accompanying his uncle on calls and particularly by the fact that his uncle had talked to him about cases as though he were an adult.

Nicholas attended primary and secondary schools in a number of communities in Pennsylvania as his father moved from parish to parish. After graduating from high school in Middletown, Pennsylvania, he matriculated at Pennsylvania (now Gettysburg) College in the autumn of 1912. In 1910 his father had taken him to attend the inauguration of W. A. Granville as president of Pennsylvania College. Granville, a Ph.B. and Ph.D. of Yale University, came to Pennsylvania from the Sheffield Scientific School at Yale, where he had been a popular instructor in mathematics. Nicholas said later that the inauguration was an event which had a great effect on the course of his life, since his decision to attend Pennsylvania College (where his uncle Harry Spangler had also graduated) was made, at least tentatively, at that time. His final decision was made partly out of loyalty to his father, but other factors entered into it too. In earlier years Pennsylvania College had been strongly denominational, but under the administration of Granville, its first president not of the cloth, it changed considerably in this regard. But in 1912, when Nicholas entered college, as now, adjustments in tuition fees were made for sons of Lutheran ministers. The Reverend Mr. Nicholas' salary in those years was hardly adequate to see a boy through four years of college.

Nicholas toyed briefly with the idea of attending the United States Military Academy at West Point, and had made some moves, through his uncle Harry Spangler, toward obtaining appointment to the class which graduated from the Academy in 1916. He took the physical examinations and visited the

Academy, but he finally decided against attending because there seemed to be nothing but peacetime army life to look forward to. He never regretted his decision in favor of Pennsylvania College, and felt later that he had made a fortunate choice and that his college had prepared him well for his professional career.

Among his college courses he had one year of mathematics (calculus), two of physics, four of chemistry (including a lecture course in industrial chemistry), and two double courses in biology taken during his junior and senior years. Chemistry and physics were taught by Johns Hopkins doctors of philosophy, one a former student of Remsen's, the other a former student of Rowland's. Dr. George Diehl Stahley, an M.D. of the University of Pennsylvania, who preferred teaching to practice, taught biology, and he permitted students to enter his courses only after they had studied at least one year of physics and two of chemistry—a practice only now, fifty years later, beginning to become generally accepted in American colleges and universities. Biology caught the young Nicholas' fancy as no other subject had, and it was thus under the influence of Stahley, "Bones" Stahley to his students, that Nicholas modified his original aims and shifted his interest from medicine to biology.

He was introduced early to independent work in biology, both in research and in teaching. As a junior in college he carried out, as extra work in an advanced physics course, an investigation on the physiological effects of light of controlled wave-length. Also, during his junior year, Stahley suggested to him that during the summer of 1915 he might study botany at the Cold Spring Harbor Laboratory under John W. Harshberger of the University of Pennsylvania, and bacteriology at George Washington University under Oscar Hunter, with a view to teaching these subjects at Pennsylvania College in the following academic year. This plan was carried out, with the result that during his senior year Nicholas was taking six courses (one the second year of the double course in biology) and teaching two, and he was listed in the 1915-1916 catalogue as an Assistant in College Biology. He received his B.S. degree at Pennsylvania College in 1916; the College awarded his father the honorary degree of Doctor of Divinity the same year.

Harshberger had suggested that Nicholas come to work with him at the University of Pennsylvania after completing his college work, but Nicholas chose instead to remain at Pennsylvania College for an additional year, taking an M.S. degree in 1917. During this year he continued to teach bacteriology and botany at Pennsylvania, holding the same title as during the previous year. He also taught beginning Latin and Greek and upper-term English at Gettysburg Academy, where for the first time he was officially called Master—a designation that was to mean much to him in another connection later.

Nicholas chose to go to Yale the following year. This was probably the most important decision of his life, after he once had decided to become a biologist, and President Granville was influential in helping him to arrive at it.

Nicholas, as a college student, had grown to know President Granville, and also his family, Mrs. Granville and their two daughters, very well. Nicholas recognized early that Granville was a thoughtful scholar, and developed great admiration for him. As a freshman he had joined a fraternity (Phi Kappa Psi) one of whose members and officers married the President's older daughter. This brought Nicholas easy entrée into the President's home, and he became a close friend of Mrs. Granville and of the Granville family. He said later that the Granvilles played an increasingly important part in his life throughout his college years. His closest acquaintance with them came during his junior year, when one of his fraternity brothers developed a lung abscess as a result of a football injury and was taken into the Granvilles' home, where the fraternity members acted as nurses for three weeks until he died. Living in the Granvilles' house under these conditions brought Nicholas even closer to the family than he had been before, and his bonds of affection to the President thus were tightened. Tight bonds of affection were always important to Nicholas, as we have intimated before.

Against this background it is easy to see why Nicholas took seriously Granville's advice to go to Yale. But the move from Gettysburg to New Haven was not an easy one to make in the autumn of 1917 when the winds of war were blowing strong. While at college Nicholas had spent a summer at the voluntary Officer's Training School founded by Leonard Wood at Plattsburg, New York. When the United States entered World War I in April 1917 he telegraphed the Adjutant General's Office in an attempt to volunteer, expecting an automatic commission as a result of his experience at Plattsburg. When he did not receive an immediate reply, he finished his year of teaching, on Granville's advice, and then spent the summer as a counselor at a boys' camp in New Hampshire. While in New Hampshire, he received a telegram from the Adjutant General's Office asking him to report for physical examination at Fort Oglethorpe. The examination was scheduled for a date two weeks before he received the telegram, according to Nicholas, and his request to take the examination at Plattsburg was refused. Granville advised him, under the circumstances, to go to Yale until called up for duty, and this he did. At least, he went to Yale; he soon called himself to duty.

He entered Yale as a graduate student and as a graduate assistant in the Department of Zoology in the fall of 1917, thus beginning an association with Ross Harrison that was to be of dominant importance to him for the rest of his life. But since Nicholas did not complete the work of that academic year, discussion of his activities as a graduate student may be deferred until after his war activities have been described.

Events had a way of turning themselves to Nicholas' advantage (which says something important, of course, about Nicholas himself), and he felt later that the failure of his first attempt to volunteer had been providential. Not willing to wait to be drafted, he enlisted in the Army Medical Corps as a private on March 5, 1918; it was possible in those days to volunteer for a particular service in the Medical Corps. He was sent to Fort Meade for basic training and was then assigned to the Vaccine Department of the Army Medical School in Washington, D.C. Here he could capitalize on his earlier bacteriological training, and he was one of several who worked to improve methods for increasing production of typhoid vaccine. Nicholas found that a type of agar used abroad as a growth medium, but with unpredictable results, consistently produced high yields if maintained at a constant pH. But when grown under these improved conditions the bacteria were sometimes atypically long, even stretching, as he described them, across the whole microscope field. He worked out a modification of the Barber device to isolate the atypical forms, developed mass cultures from the isolates, injected them into cats, which developed symptoms of typhoid, and then isolated from the cats typhoid bacilli normal in form. I do not know whether these discoveries were turned to the advantage of the American Expeditionary Forces, but they serve to illustrate the scientific ingenuity that already characterized Nicholas' mind.

Nicholas was discharged from the Army on January 9, 1919. He was later, from 1924 to 1936, to hold a commission as First Lieutenant in the Sanitary Officers Reserve Corps. On his discharge from the Army in 1919, however, he returned to the Osborn Zoological Laboratory at Yale. As a graduate student, as a graduate assistant in his earlier years, and as Currier Fellow in his final year of graduate study, he was a hard worker, and already at that time he became very devoted to Harrison, concentrating anxiously on measuring up to the high standards of workmanship set by Harrison for all members of the laboratory. While he was a graduate student, the laboratory was literally his home; he lived in quarters for graduate students established in one of its towers. The laboratory represented a figurative home to him for most of his subsequent life; only once was he officially to leave it again for any appreciable number of years, and even then he worked there during at least some of the summers.

Nicholas received his Ph.D. in 1921; he went to the University of Pittsburgh in the autumn of 1921 as Instructor in its Department of Anatomy. Shortly after, on December 17, 1921, he married Helen Benton Brown of New Haven, who survives him. He spent five years at Pittsburgh, one as Instructor, then four as Assistant Professor. The work of these years had a very special character of its own which proved important to his further development as a biologist.

Nicholas was invited to come to Pittsburgh by Davenport Hooker, who had been the first student to earn a Ph.D. with Harrison at Yale. Hooker also had a number of connections with Nicholas, other than through Harrison, that may have brought Nicholas' qualities to his attention. In 1917 Hooker had married Helen Ferris, the daughter of Harry Burr Ferris, who taught gross anatomy at Yale; for many of Harrison's years at Yale it was a requirement of the Department of Zoology that minors be elected outside the Department, and a number of the students, even as late as the 1930s, elected to take part of their minor work in human anatomy at the Medical School. Nicholas did so; the course under Ferris' direction was a particularly lively intellectual experience—Hooker said of Ferris in a memorial note that, when he taught, bare bones seemed to take on flesh before the students' eyes—and was highly stimulating to Nicholas. Hooker himself spent his summers in Clinton, Connecticut, and may well have seen Nicholas in the dissecting room at Yale. Furthermore, Mrs. Hooker's uncle Richard Shelton Kirby had taught at Gettysburg during Nicholas' first three years there and had known him. In 1915 he moved to New Haven where he lived when Nicholas was a graduate student; his house was another meeting-ground for Hooker and Nicholas when the latter was a graduate student.

Hooker was head of the Department at Pittsburgh when Nicholas came there; John Donaldson, the son of H. H. Donaldson so distinguished for his work on the nervous system of the rat, arrived the same year as Nicholas. The working conditions at Pittsburgh were almost unbelievably primitive at the time; according to Donaldson, the laboratory in which Nicholas worked would not now be acceptable as a janitor's closet. Its sole plumbing, a single sink, was installed personally and conjointly by Hooker, Donaldson, and Nicholas, who also cooperated in such activities as inventing bookstands for the dissecting room based on movable No Parking signs, which still remain in the Department, and establishing a flourishing rat colony, as a natural result, John Donaldson said, of family background. The rats lived in a penthouse on the roof. Next to them, in a little hut, were kept cats that Nicholas was using for endocrinological experiments to be described below; the cats learned to find unsealed areas in the baseboards and vanished into the very thick hollow tile walls of the building to be retrieved four floors below, hungry but undamaged, when their yowling indicated their positions. Yet Nicholas enjoyed some of his most productive years in these surroundings; small wonder that in later years his colleagues' expressions of dissatisfaction with more modern facilities did not distress him to the degree that the complainers might have wished.

Hooker, Donaldson, and Nicholas were a remarkable team;

they were co-equal not only as plumbers and animal caretakers but also as instructors. Each of the three taught one section of the first-year anatomy course, and each taught his section as he thought best, with one of the other two as assistant. There was no limitation except that a certain portion of the work had to be covered in the allotted time; whoever assisted would loyally carry out the ideas of the principal teacher of the moment. No teaching experience could have been better designed to stimulate the imagination of one as independent and eager as the young Nicholas.

The course was also unique in that it seems to have been the first in the country to combine gross, microscopic, and developmental anatomy into a single unit. This too had its historical backgrounds: as a result of Harrison's German training, the influence on him of Gegenbaur's concepts, and his own large view of things, his students learned vertebrate morphology as an integrated discipline interrupted by no artificial barriers between embryo and adult or between cell, organ, and organism. Donaldson had studied pathology with Welch, who had dealt with all its phases, gross and microscopic, as a unified subject. Working to integrate many seemingly disparate facts and ideas would have been particularly satisfying for Nicholas, whose life always encompassed multifold activities simultaneously.

Although the five years at Pittsburgh were the only ones that Nicholas spent within the confines of medical school walls, he remained close to medical thought throughout his life. He was a wise adviser at Yale to countless premedical students; for many years he was an examiner for the Connecticut State Board of Healing Arts. His whole philosophy of medical education, in which he always maintained a keen interest, was based on his Pittsburgh experience.

The Pittsburgh years were also particularly favorable for the development of Nicholas' research. Nicholas taught not only the combined anatomy course to first-year students but also, for four years, neuroanatomy to second-year students, which reinforced his already growing interest in the nervous system. His needs for uninterrupted time for his own work during the *Amblystoma* breeding season were recognized and honored. Equally important, the rat colony that had been set up through the cooperative efforts of Hooker, Donaldson, and Nicholas provided abundant material when Nicholas began to perform his experiments on rat embryos.

In spite of the success of his work at Pittsburgh, Nicholas nonetheless returned in 1926 to the Department of Zoology at Yale as Assistant Professor, and he remained in the Department for the rest of his life. He was promoted to Associate Professor of Comparative Anatomy on the Bronson Foundation in 1932, and was appointed in 1935 to the Bronson Professorship of Comparative Anatomy. This was the chair in which Harrison had been the first incumbent when he had come to Yale from The Johns Hopkins University in 1907. Harrison had vacated this chair to become Sterling Professor of Biology in 1927. Nicholas had fewer years to wait for the appointment to a Sterling Professorship in Biology. He received it in 1939, and held it until he became Emeritus in 1963. He was Chairman of the Department of Zoology from 1946 to 1956, and Master of Trumbull College from 1945 until his retirement.

He devoted much of his time and many of his energies (and they were plural) throughout the years to duties other than those directly related to his own teaching and research, but from the time he began his research activities as a graduate student at Yale he felt his research to be by far the most important of his varied interests. Accordingly, it is appropriate to devote the central section of this memoir to a consideration of the varied subjects of his investigations.

Embryology was the primary one, and in fact he chose to study at Yale, under Granville's advice, as the result of an express desire to work with Ross Harrison in this field. Harrison had, by the time Nicholas began his embryological studies, performed important pioneering experiments on the development of asymmetry in the vertebrate limb. Using embryos of the spotted salamander, *Amblystoma punctatum,* as it was then officially known, he had shown that whether a forelimb rudiment would form a left or a right limb is determined in some respects by the relationship of the limb rudiment to its surroundings in the embryo. At the stage at which Harrison worked, a rudiment of the forelimb develops into a limb corresponding to its side of origin if its dorsoventral axis is placed in normal orientation with respect to the host, and into a reverse limb if this axis is inverted at transplantation. These rules hold whether the grafted limb is placed on its side of origin or on the opposite side of the body. Harrison had found that in some cases, even though the transplanted limb rudiments followed the above generalization, the limbs regained their normal posture later by adjusting their position. In the work for his dissertation Nicholas attempted to analyze the factors responsible for such regulation of posture. His experiments altered the location of the grafts, their size, their age at transplantation, and the degrees of rotation through which they were moved before transplantation. These experiments were thus simple variations of those already performed by Harrison, who had rotated his grafts through 180°. Nicholas rotated the disc representing the limb rudiment through either 90° or 270° before transplantation. He found that the limbs resulting from 90° rotation recovered their typical posture by rotating counterclockwise, and those resulting from 270° rotation rotated clockwise (thus in each category through the shorter arc). He showed that the factors instrumental in effecting the rotation related primarily to the development of the skeletal limb girdle.

The definitive results of Harrison's experiments were presented in a highly influential publication that appeared in 1921. Nicholas, as we have said, was awarded his doctor's degree in 1921, but the paper based on his dissertation did not appear in print until 1924. It has been stated in another memoir of Nicholas that the delay resulted from Harrison's perfectionism and that the thesis was repeatedly rewritten before its publication. This explanation is not complete. It is quite true that Nicholas' writing has on occasion come under some criticism. His mind worked with great speed, and as a result he sometimes expressed himself, both orally and in writing, elliptically and somewhat unconventionally, but his ideas were expressed with great vigor, and readers of his papers cannot escape feeling the force of his intellectual power. With respect to the delay in publication of the dissertation, comparison of the original dissertation with the published version shows that, although the latter is considerably shorter than the original, there were few drastic literary changes; the real difference between the two versions resides in the content. Nicholas had performed extensive additional experiments, differing from his original ones in the number of degrees through which the grafts were rotated, before completing the paper for publication.

Both in the dissertation and in the 1924 publication based upon it, Nicholas stated that experiments had been performed in which the immediate surroundings of the limb were rotated, but that these experiments were still incomplete and would be described later. The experiments, which involved a double operation, were ingenious; preliminary results were reported at the December 1921 meetings of the American Association of Anatomists, and the abstract states that, when the limb bud is oriented normally with reference to the embryo but the surrounding tissue rotated, the limb develops in such a way that it assumes its posture with reference to the surrounding area and not to the organism as a whole. A progress report on this work was delivered to the American Society of Zoologists at its December 1924 meetings, and some further details relating to the development of the limb girdles after such experiments were presented at the April 1926 meetings of the Anatomists. The results and the experiments were never described fully in print, although some of them were incorporated in a chapter of a compendium volume on experimental embryology published in 1955. Nicholas' final publication describing the effects of rotating the surrounding tissues on the asymmetry and posture of the limbs did not appear until 1958, more than thirty years after the experiments were performed. The results, however, were known to investigators of limb development and were frequently referred to earlier in the literature. In fact, the experiments were carried further by F. H. Swett who reported in 1938 that the effective portion of the surrounding tissue is that originally dorsal to the limb rudiment; he explained the results in terms of a barrier set up here against the actions of factors resident in various other parts of the embryonic body. The facts that Nicholas himself had not carried this experimental analysis to an end, and that he did not publish until 1958 the results of experiments begun in 1921, are easily accounted for. He was either completing or beginning too many new experiments of other kinds to be able to devote further attention to the earlier ones.

As a matter of fact, some of the varied paths into which he diverted his energies led from the same points of origin as the work for his dissertation, and he began to follow some of them out before the work of his dissertation was very far under way. Even as a graduate student he did not choose to concentrate his efforts on a single problem. During the academic year 1918-1919, thus presumably immediately after returning to Yale from the Army, he made, at Harrison's suggestion, limb bud grafts to the dorsal or ventral midline. It would seem that these must have been among Nicholas' first operations; in the memoir of S. R. Detwiler that he prepared for the National Academy of Sciences he wrote that Detwiler gave him his first lessons in surgery on *Amblystoma* in the spring of 1919. Theoretically, it would have been expected that the midline grafts, if their anterior-posterior axes conformed to those of their hosts, would form double limbs, each component of the pair with its asymmetry corresponding to the side upon which it develops. If the anterior-posterior axis of the bud is reversed, the resultant limbs should show reversed asymmetry. Nicholas reported the successful performance of such experiments, with a few grafts showing the predicted results, at the December 1921 meetings of the Anatomists; the definitive publication appeared in 1924, five months before the article based on his dissertation.

Meanwhile Harrison and Detwiler had been studying for some time the relationships of the nervous system to transplanted limb buds; in fact, Harrison's motive in his first amphibian limb bud transplantations (1907) had been to investigate their bearing on the development of the nervous system. Nicholas, in his 1924 paper on limb bud grafts to the dorsal midline, made some preliminary observations on the effect of these grafts on the underlying spinal cord. As a result of these observations he performed further experiments in which grafted limb buds were utilized as barriers isolating portions of the central nervous system. Detwiler had studied in other ways the effects of the medulla on the differentiation of the spinal cord, and Nicholas saw that the interposition of the limb as a barrier between different parts of the nervous system could further elucidate such effects. A long article by Nicholas published in 1929 in the Festschrift in honor of Hans Spemann's sixtieth birthday reported an analysis of the responses of parts of the *Amblystoma* nervous system isolated in this way. This paper reported the use of limb grafts to separate the medulla from the spinal cord or to fill gaps caused by the removal of the segments of the cord which innervate the limbs. In experiments forming the basis of another paper, published the following year (1930), the mesencephalon was removed and limb bud grafts were used to block the later junction of diencephalon and medulla. These experiments were not followed by quantitative changes in the first five segments of the cord, and thus confirmed Detwiler's earlier demonstration that the medulla is the effective portion of the central nervous system influencing the proliferation of cells within the cord. In 1931 Nicholas described in short notes the effects of transplanting an extra medulla; these, again confirmatory of earlier results by Detwiler, seem not to have been described *in extenso*. Nicholas' last report on transplantations within the amphibian central nervous system appeared in 1956; this was a short paper in the *Proceedings of the National Academy of Sciences* describing the effects of reversing strips of neural plate together with underlying chordamesoderm; the degree of regulation which followed varied according to which of the axes were reversed.

There was another set of sequels, in Nicholas' work, to the experiments that he began in 1919 by transplanting limb bud grafts to the dorsal midline. In his preliminary report of these experiments (1922), and in the 1924 paper describing them more fully, he recorded the observation that these limbs were innervated by nerves which do not normally supply them. Nicholas first reported in 1928 innervation of the dorsal limb grafts by cranial nerves, and in 1929 he published a preliminary note dealing with movements in ectopic limbs (including some developing in the orbit of the eye) innervated by cranial nerves. A long paper in 1933 dealt with the correlation of nerve supply and the movements of the transplanted limbs. The last paper Nicholas published on limb movements was written in collaboration with D. H. Barron, and reported the results of electrical stimulation of dorsal and ventral nerve roots of normal and experimental axolotls of about six months of age. These results emphasized the importance of sensory components in coordinating the activity of groups of muscles.

The significance of the studies on developing embryos described above, closely related to studies on these subjects by Harrison, Detwiler, and Swett, was that they contributed to the growing body of knowledge on limb asymmetry, posture, innervation, and movement. Nicholas, however, also carried out numerous other analyses of amphibian life and development. His very first publication, an abstract of a paper delivered to the Zoologists in December 1920, was a note verifying the fact that *Amblystoma tigrinum* reacts to olfactory stimuli; the experiments on which this was based, carried out at the instigation of Henry Laurens, were begun, like the experiments on limb transplantation, during the spring of 1919, and Nicholas' first definitive paper, published in 1922, described these experiments and their results. Then he recorded in 1924 and 1925 observations on the presence of a balancer in *Amblystoma tigrinum,* a species previously described by others as lacking this organ. These were modest studies, but they serve to show that the diversification of Nicholas' biological interests began very early during his scientific career.

Although he later moved farther afield among the vertebrates, Nicholas never abandoned his interest in the development of *Amblystoma.* In 1945 and 1948 he reported the results of studies, carried out by vital staining, on endodermal movements in this form during pregastrular stages; these were important and original in that they pointed up the need for investigation of morphogenetic movements during blastula stages, hitherto largely neglected. In 1952, when embryology was entering its present biochemical phase, he collaborated with Edith Krugelis in an investigation of the effects of temperature on alkaline phosphatase activity and nucleic acids in *Amblystoma;* variations in temperature were shown not to produce alterations in the phosphatase activity nor in DNA production, but lowering the temperature increased the production of RNA under the conditions of the study. In 1963 he published a paper describing movements of the surface pigment of cleaving *Amblystoma* eggs as studied by time-lapse cinephotomicrography; this was his last full paper to appear. Four years before, he had published an earlier paper on this subject reporting investigations begun in 1926 or 1927 and continued intermittently ever since, and in the 1959 paper he stated that his original interest in this problem had been stimulated in the 1920s by comments of Harrison on normal development.

Thus his work on amphibian development began and ended in ideas emanating from the work of Harrison. This was not always to be the case for his investigations in other than amphibian embryology, and to consideration of these we may now proceed. It must be evident from the foregoing paragraphs that Nicholas' fashion of work was not such as to permit the construction of an orderly chronological record of his investigations. Accordingly these may be (as they are here) arbitrarily classified on the basis of the vertebrate groups he studied and the problems raised by their development.

Let us first take up his contributions to teleost embryology. He had made his first visit to the Cold Spring Harbor Laboratory, it will be remembered, during the summer following his junior year at college. In 1925 he returned to the Laboratory for the summer as an assistant in Comparative Anatomy; the following summer he assisted in courses in Comparative Anatomy and Experimental Surgery, and in the summer of 1927 he headed the course in Surgical Methods in Experimental Biology (and in this year he became a member of the Scientific Advisory Committee of the Laboratory, a membership which he maintained through 1940). By 1927, his fourth summer at the Laboratory, he was unable to resist the challenge offered by the marine embryos available there, and accordingly he turned his attention to the study of the development of *Fundulus heteroclitus.*

The eggs of this common minnow, the killifish, had previously been subjected to study only by indirect methods, since its shell, the so-called chorion, had previously seemed impossible to remove without injury to the egg. By devising a clever method, still used by a number of investigators of fish development, of dechorionating the egg with especially modified eye-surgeons' iridectomy scissors, he made it accessible to direct microsurgical manipulation; thus he began the modern studies on fish eggs in America. A description of the method he used for removing the shell was published in the autumn of 1927; again, conforming to a familiar pattern, final publication of the results of the experiments was deferred until 1942, when they were presented in an article published jointly with the author of this memoir, one of his former students. All the experiments on premotile stages described in this paper were performed by Nicholas. These were defect experiments, but they were far more refined than defect experiments previously performed on *Fundulus* eggs by others, who had merely poked needles through the intact chorion. Nicholas' results demonstrated the powers of regulation inherent within the developing teleost egg. Investigations of teleost development, described in publications which appeared almost simultaneously in the 1930s in Europe and in the United States, were among the first to broaden Spemann's concepts of embryonic induction to include other than amphibian development. Had Nicholas' 1927 results been fully published earlier, he would have received the credit he deserved for being the first to apply modern methods of experimental embryology to the study of teleost development.

He also applied such methods to the study of mammalian development. His experience with mammalian experimentation dated back to the time of his early years at Pittsburgh. During the summer of 1923, when he was visiting Mrs. Nicholas' family in New Haven, he often came to the Osborn Laboratory to read journals. Dr. W. W. Swingle, then Assistant Professor of Biology at Yale, asked him if he would like to give him a hand removing parathyroid glands from cats. Nicholas accepted the invitation with alacrity. He was so skillful at the surgery that Swingle invited him to collaborate with him on a detailed study of parathyroid tetany in cats.

Swingle and Nicholas began by extirpating the glands in the cat. Before 1925, when Collip and his collaborators first reported the endocrine function of these glands, the literature contained conflicting reports concerning their dispensability in the cat. Swingle and Nicholas demonstrated that complete parathyroidectomy is invariably fatal in the cat, and that the survival of some cats after apparently complete parathyroidectomy is accounted for by the presence of accessory glands that have not been removed. They reported, also, the results of auto- and homo-transplantations of the gland, demonstrating the successful survival and function of the autoplastic grafts.

Preliminary reports on these experiments appeared at the end of the year 1923. According to Swingle, Nicholas contributed generously of his time and energy in this collaborative work, which continued through several years, and Swingle thinks that the work might never have been completed without Nicholas' suggestions, operative skill, and unflagging interest. That Nicholas made this substantial contribution to endocrinological progress was probably remembered by only a few of his friends during his later years, and may come as a surprise to some of his younger colleagues, although a number of students participated in his graduate course in endocrinology during the years he taught it at Yale.

The last of the joint publications with Swingle on the parathyroids appeared in 1925, but Nicholas' knowledge of endocrinology was useful in various ways in his later work on mammalian development. Methodologically it was of advantage to him. In his first paper on mammalian development, also published in 1925, he referred specifically to a surgical procedure used by Biedl, to whose work Nicholas had referred in the papers on the parathyroids. Also, for the handling of mammalian embryos *in vivo* and *in vitro,* an understanding of the role of endocrine factors in reproduction is essential, on theoretical as well as practical grounds. Nicholas was later to deliver several talks at scientific meetings on various aspects of reproductive physiology in the rat, and during the 1940s he published two papers reporting the results of work in this area. One of them was a joint publication with J. A. Carmosino, who died before the paper appeared in print. Carmosino had been for over fifteen years the caretaker of Nicholas' animal colony at Yale; Nicholas' manner of working with him was such that he had not only been a devoted assistant but had become an active participant in the work itself.

Nicholas' 1925 paper on the application of experimental methods to mammalian embryos states explicitly that the developmental investigations were begun at Pittsburgh in 1923, and it gives this reason for starting them: "Recent studies upon the transplantation of eyes in adult mammals by Koppányi ('23) have rendered it imperative that more should be known about the early mechanics of development in the mammal." One of Nicholas' colleagues at Pittsburgh remembers how skeptical Nicholas was of Koppányi's results at the time they were published; thus there is little reason to doubt that their publication was in fact the event which stimulated Nicholas' initiation of his own studies on mammalian development.

His investigations on mammalian eggs, embryos, and fetuses were carried out almost exclusively with the rat. When the 1925 methodological paper was sent to press, Nicholas knew that E. A. Swenson had published a paper the same year concerning methods of procedure in studying mechanical and electrical stimulation of rat embryos. By the time Nicholas published his second paper on mammalian development the following year, he had seen Ernst Bors's 1925 publication which also described the application of experimental methods to the study of mammalian development, this time in the rabbit. Thus Nicholas was one of the first investigators to work in this field, and his studies were begun independently without knowledge of the fact that others were developing similar interests. Nicholas was the only one of the three initial workers to carry out a substantial program, and he continued it actively throughout the rest of his life. Of all his varied embryological studies, his experimental analysis of the development of the rat was probably of centralmost interest to him. Performing the delicate operations on rat embryos was probably the greatest pleasure in Nicholas' life, and he enjoyed carrying out the experiments more than writing about them. Furthermore, the experiments were diverse; various types of experiments were carried out simultaneously; and new kinds of experiments were often begun before older ones were written up. Thus again, as in the case of the amphibian studies, they are difficult to discuss on a chronological or any other systematic basis.

It seems clear from the record, however, that Nicholas' first experiments on mammalian material were extirpations of the limb, the eye, or the tail at relatively late fetal stages, that is, between one and nine days before birth. The first paper (1925) discussing the results of these experiments demonstrated that, during the final third of gestation, amputation of the limb is not followed by regeneration; this was the experiment Bors had reported for the rabbit with the same result. The result, of course, simply suggested to Nicholas that he must study earlier stages of development, which he soon was to do, but meantime there was still at least one major problem to be investigated by the methods he had developed for experiments on the older fetal stages. This was to ascertain the results of spinal cord section in fetuses, and this investigation was carried out jointly with Davenport Hooker, who was senior investigator during this collaboration. The operative procedures and the testing of the living fetuses were performed by Nicholas; Hooker examined the sections and interpreted the histological findings.

The first reports on these experiments, and their interpretations, were made in 1927; Nicholas had by then developed his own interest in the nervous system, and since 1915 Hooker, with positive results, had been studying in frog embryos the regeneration of the spinal cord transected early in development (closed neural-fold stage). The cord transections on the rats were made on embryos and fetuses at between twelve to eighteen days of gestation, either by cutting or by electrocautery, and the results were negative with respect to regeneration. Some previous authors (including Gerard and Koppányi in 1926) had tentatively claimed, on the basis of physiological tests alone in the absence of histological study, that cord regeneration might occur after transection in mammalian fetuses. Hooker and Nicholas were able to explain away the physiological results which led to suspicion of regeneration on the basis of transmission of impulses along collateral paths. Although abortive regeneration has subsequently been demonstrated in the spinal cord of rats, a man or other mammal whose cord is traumatically severed may still expect to remain paralyzed below the site of the injury for his lifetime.

Before the study with Hooker was completed, Nicholas had begun other types of experiments on rat fetuses. In 1929 he published a short communication describing attempts to transplant the eye from one fetus to another. Two years later (1931) he reported attempts to maintain rat embryos of eight to nine days of gestation age in various conventional salt solutions *in vitro* or in various ectopic positions in the mother: he placed a horn of the uterus in a subcutaneous pocket in the body wall; he separated the upper tube from the uterus three days after fertilization, releasing segmenting eggs into the abdominal cavity; he transplanted eight- and nine-day embryos to the outside body wall, to the femoral fascia, and to various subcutaneous areas. Some degree of differentiation occurred, the best in transplants to the mammary gland, and Nicholas commented in a brief paper in 1931 that the grafts resembled the chick grafts described by Willier and Murphy after transplantation to the chick chorio-allantois.

In 1930, at the invitation of Willier, Nicholas spent one of his rare summers away from New Haven teaching comparative anatomy and experimental morphology at the University of Chicago. Here he saw chick chorio-allantoic grafts at first hand. He later encouraged Dr. Dorothea Rudnick, who had in the meantime received her degree with Willier and who was an expert at chorio-allantoic grafting, to come to Yale to work with him, and thus began a fruitful collaboration.

In 1931 a short paper and in 1933 a longer one, both published jointly by Nicholas and Rudnick, described the development of rat embryos grafted to the chick chorio-allantois. Next, Nicholas and Rudnick began to work on the development of rat embryos *in vitro.* They described in 1934 and again in 1938 the development of embryos of egg-cylinder to head-fold stages explanted to a culture medium composed of rat plasma and rat embryo extract, and they reported that some differentiation occurred. They also described briefly in 1937 the explantation *in vitro* of transverse pieces of nine-day rat embryos, but did not feel that the degree of progressive differentiation attained in these experiments warranted pursuit of the subject. Nicholas' next-to-last publication was an abstract of a paper presented at the 1963 meetings of the Anatomists describing, jointly with Bette Duff, the development of such fragments in the anterior chamber of the eye.

Nicholas designed a special chamber that permitted the circulation of fluids for studies *in vitro* (1937) and in 1938 he reported that the use of this chamber improved the differentiation of explanted rat eggs and embryos. Also, he published a number of extensive papers in the 1930s and 1940s (and one in 1950) on the potentialities of rat embryos for development after transplantation to various abnormal sites *in vivo.* These were summarized in the 29th Mellon Lecture, delivered at the University of Pittsburgh School of Medicine in 1946; the lecture was published in revised form in the *Quarterly Review of Biology* the following year.

According to Dr. Rudnick, who collaborated in much of the work, the transplantation and explantation experiments agreed in showing that the period of early axis formation in the rat blastocyst (*ca.* nine to ten days after insemination) was the most favorable moment at which to secure progressive differentiation outside the uterine environment. The extent of progress possible was of the order of some two to five days of normal development. In the grafts, differentiation of the established germinal regions was predominantly at the tissue level. *In vitro,* morphogenetic changes,—e.g., folding, outgrowth, somite formation, etc.—

tended to parallel or even outpace tissue differentiation. All these experiments were essentially exploratory and were dropped when it became clear that only limited development was to be obtained in the various experimental environments devised at that time. Nicholas' hope had been to find an accessible situation where the mammalian embryo could be carried through, if not to term, at least to a stage of active neuromuscular function.

Nonetheless, the application of the methods of experimental embryology to mammalian eggs and embryos would seem to have been Nicholas' most important direct scientific contribution. Perhaps his most significant set of experimental results in this area remains to be specified here. One of his graduate students, B. V. Hall, in studying the changes occurring in the uterus during pregnancy, found that the *zona pellucida* of the rat's egg softens in acidified calcium-free Ringer's solution; this permitted for the first time experimental separation or fusion of blastomeres in the mammal. Nicholas and Hall (1942) demonstrated that blastomeres isolated at the two-cell stage and then transplanted into the uterus could develop to the egg-cylinder stage, and in a single case an oversized fetus seemingly produced by the fusion of two one-celled eggs was brought to term. These truly significant results, which proved the regulatory nature of mammalian development, have not received due attention in the subsequent literature. When Seidel first reported in 1952 the development of isolated rabbit blastomeres, he did not mention the work of Nicholas and Hall; in Seidel's long definitive paper (1960) the Nicholas and Hall paper is listed in the bibliography but not mentioned in the text.

During the 1940s, Nicholas' studies on the mammal, like those on the Amphibia previously reported, took a biochemical turn, and a series of excellent collaborative studies, with Heinz Herrmann, on the biochemistry of developing rat muscle was completed. Nicholas also studied, together with E. J. Boell, the respiratory metabolism of developing rat eggs from the one-cell through the sixteen-cell stage by means of the Cartesian diver technique.

Also, as a corollary and necessity to his experimental studies, he worked out a series of normal stages for rat development. The stage series was described briefly in a chapter contributed by Nicholas to a compendium volume on *The Rat in Laboratory Investigation* (1942, 1948). He prepared photographic illustrations of the stages in 1935, and a small number of bound sets of these, dedicated to Harrison, were privately distributed, but unfortunately the detailed rat stage series, like that previously prepared by Harrison for *Amblystoma,* was never formally published.

A few words might be mentioned here as to Nicholas' technical ingenuity and skill. It may be implicit in what has already been said that his manual dexterity was exceptional, and that his imagination was fertile in enabling him to devise technical improvements and innovations, beginning at least as far back as his time as a private in the Medical Corps. Visitors to his operating room for mammalian surgery at Yale will remember that he had invented a foot-focusing device for his dissecting microscope long before such an instrument was on the market, and that he had adapted a foot-treadled Singer sewing machine as an integral part of an apparatus for artificial respiration of rats. He invented a microscope lamp, valuable for use with dissecting microscopes, that sharply focuses cool bright light within a restricted microscopic field; this is currently manufactured and marketed as the Nicholas Illuminator by the Bausch and Lomb Company, and is widely used in industrial as well as research and academic laboratories. He was also exceptionally adept at photography and in fact published a paper, in the mid-thirties, on biological photographic illustration. But his long bibliography, numbering over 135 publications, includes only one or two entries dealing with purely technical aspects of biological teaching or research. It is to his credit, considering the pleasure with which he used his hands and his tools, that in years during which addiction to gadgetry was becoming an increasingly prevalent laboratory disease, he was never seduced by the temptations of instrumentation for its own sake. His primary interest was in experiments.

The subjects of the dissertations of the graduate students who worked with him for their degrees—over twenty, including several whose work was directed jointly with other members of the department—reflected Nicholas' own interests, embryological, endocrinological, and neurological, and accordingly were as varied as were Nicholas' own investigations. He encouraged his students to think and work independently, sometimes, at first, to their exasperation, and many of them developed new and important fields of investigation after receiving their degrees; a number of them occupy key positions in American biology and medicine.

Nicholas' teaching activities were confined principally to Yale. When the Rockefeller Institute became a graduate school, he did hold one of the early appointments there: he was a Lecturer in the Institute for the academic years 1955-1957 and Visiting Professor during the academic years 1957-1958, 1958-1959, and 1960-1961. But though he limited his teaching to a few institutions, his influence spread wide through a variety of other activities that he carried on over and above his strictly academic duties. These were so diverse that they too are difficult to discuss chronologically.

At Yale itself, Nicholas was not only a member of the multitudes of committees upon which faculty members are so often called to serve, but he also held a number of important administrative positions. He was a member of the Board of Trustees of the Sheffield Scientific School from 1940 until 1963, and

Secretary of its Board from 1941 to 1956. Of equal importance, on a different level, was his mastership of Trumbull College. In 1933, when the colleges were established at Yale, he was elected one of the original Fellows of Trumbull; in 1945 he became its Master. He continued in this position until he retired. He enjoyed intensely his administrative duties in the College, and especially his advisory relationships with the students. Together with Mrs. Nicholas he provided warm hospitality for the members of the College. While Master of Trumbull, Nicholas established close relationships between Trumbull College and St. Catherine's College, Cambridge University; he became, in 1955, an Honorary Fellow of St. Catherine's.

But, to him, the most important administrative position he held at Yale was the chairmanship of the Department of Zoology. When Harrison retired in 1938, Lorande Loss Woodruff succeeded him as Chairman. Nicholas assumed the chairmanship in 1946 when Woodruff retired from it.

As already remarked, Nicholas became deeply devoted to Harrison early in his career as a graduate student. His admiration and affection for him grew continuously throughout the years; as a result, appointment to the chairmanship of the department that Harrison raised to such high eminence marked to Nicholas the acme of his career. He retained the chairmanship until 1956.

Those of his outside commitments that were most closely related to his academic life were editorial in nature; he held a number of important editorships. He served a stint on the Editorial Board of the *Journal of Morphology* (1933-1936); he was an advisory editor for one of the sections of *Excerpta Medica* (Anatomy, Anthropology, Embryology, and Histology) from 1947 until his death, and consulting editor for the *Yale Journal of Biology and Medicine* (1949-1954); he was also President of the Board of Managers of the last-named from 1952 until 1962.

From 1938 to 1963 he was Editor of the section on Vertebrate Embryology of *Biological Abstracts,* and from 1940 until his death he was a member of the Administrative Board of the *American Anatomical Memoirs* published by the Wistar Institute of Anatomy and Biology. But to him the most important of his editorial functions were those he performed for the *Journal of Experimental Zoology.* The *Journal* was established in 1904, and Harrison was its first Managing Editor, a position which he retained until 1947. Although it was only in 1946 that Nicholas became a member of the Editorial Board of the *Journal,* Harrison had previously often consulted him about manuscripts submitted to the *Journal.* Accordingly, Nicholas had had substantial experience in reviewing manuscripts when in 1947 he succeeded Harrison as Managing Editor. Harrison continued as a member of the Editorial Board, and Nicholas in turn sought his advice about many manuscripts. Nicholas retained the post of Managing Editor until he died.

When the *Journal* was founded, experimental zoology was new and seemed a unified science. By the mid-forties, there was little new or unified about experimentation on animals, and new journals were rapidly being set up to cover areas formerly the subject of publications in the *Journal of Experimental Zoology.* Nicholas' ambition as Managing Editor was to emulate the standards set by Harrison. It was no mean feat, when zoology was losing its identity as a single unified science, to maintain the *Journal,* as Nicholas did, as one of the leading biological journals of the world.

Nicholas belonged to a number of fraternities and honorary societies: Phi Beta Kappa, Sigma Xi (National Executive Committeeman, 1954-1959; President, Yale Chapter, 1930-1931), Phi Kappa Psi, Gamma Alpha, Beta Beta Beta, Phi Beta Pi; he was a member also of the Torch Society and of Berzelius at Yale. He was an active member of many professional societies, local, national, and international: the American Physiological Society, the American Society of Zoologists, the American Association of Anatomists (Executive Committee member, 1947-1951), the Society for Experimental Biology and Medicine, the American Cancer Society, the American Association for the Advancement of Science (Fellow), the American Society of Naturalists, the Biological Photographic Association, the Society for the Study of Development and Growth, the Connecticut Academy of Arts and Sciences, the Beaumont Club at Yale University (President, 1951), the New York Academy of Sciences, the New York Zoological Society (Fellow, and, from 1944 on, a member of the Society's Scientific Advisory Council), the International Institute of Embryology (Fellow, and, from 1961 until his death, a member of the organizing committee for its 1964 International Conference), and the International Society for Cell Biology (Secretary, VII International Congress of Cell Biology; member of Executive Committee, 1951-1957; assistant treasurer, 1951-1963). He was a member of the Advisory Board of the Wistar Institute from 1939 to 1952 when the Board was dissolved, and for the years 1956 through 1958 a member of the Biology Visiting Committee of the Brookhaven National Laboratories. His connections with the Cold Spring Harbor Laboratory have already been specified; he was a life member of the Bermuda Biological Station. He was elected to the American Philosophical Society in 1946 (Councillor, 1954-1957), and to the American Academy of Arts and Sciences and to the National Academy of Sciences in 1949. From 1955 to 1958 he was Chairman of the National Academy's Section of Zoology and Anatomy.

Nicholas' activities on the Washington scene were far from limited to membership in the Academy and serving a term as chairman of an Academy section. He played a large number of administrative roles under the ægis of the Academy and the National Research Council, and others farther afield.

In 1942 he was appointed by the National Research Council Executive Board as chairman of a committee on zoology of the Division of Biology and Agriculture of the National Research Council, but the Council has no record that the committee ever met. From 1948 to 1954 he was a member-at-large of the Division of Biology and Agriculture; he was Chairman of the Division from February through June 1948; in 1948 he became Vice Chairman. His term in the last office ended in 1952. He was also a member of the Executive Committee of the Division from February 1948 through June 1952.

He was a member at various times of a number of National Academy of Sciences–National Research Council committees. He served from April 1947, when it was first established as the Committee on UNESCO, through December 1959, on the National Research Council Committee on Science in UNESCO. From 1949 to 1952 he was a member of the U.S. National Committee of the International Union of Biological Sciences, and from 1959 until he died he was a member of the Evaluating Committee of the National Academy of Sciences–National Research Council for the National Aeronautics and Space Administration Postdoctoral Research Associateships.

In addition to participating in these activities related to the National Academy and the National Research Council, he was also active in the National Science Foundation in its early days. The Foundation was established in 1950; it appointed its first divisional committee members in its fiscal year 1952 (which began in July 1951) and Nicholas was listed as a member of the Divisional Committee for Biological Sciences for the fiscal years 1952 and 1953 (that is, from 1951 to 1953 calendar years).

This already formidable list of Washington duties has so far omitted his participation in the two fields of extracurricular administration in which he was most interested, and which deserve to be discussed in greater detail; these activities, related to biological organizations and to personnel, began with duties assumed at the request of the National Research Council, but expanded to exert an influence well beyond the limits of their origin.

The first of these interests, which was to prove of particular significance to biologists, led to the establishment of the American Institute of Biological Sciences. A group of nine biologists, of whom Nicholas was one, wrote in August 1946 to Robert F. Griggs, then Chairman of the National Research Council Division of Biology and Agriculture, requesting that the Division take action in developing such an institute. In November 1946 a Committee on the Proposed Institute of American Biologists was appointed by the National Research Council to assist in organizing the Institute, and Nicholas was a member of this committee. His views were of particular value to it as a result of his having been President of the American Biological Society during the previous year (1945). This society had, according to Nicholas, originally been set up to aid *Biological Abstracts,* but had in time expanded its sphere of interest sufficiently to draw up, together with the Union of American Biological Societies, of which Robert Chambers was then President, a program for an organization that would aid biologists and biology more generally. This program had been published, under the authorship of Nicholas and Chambers, in the *American Naturalist* in February 1946. The Committee on the Proposed Institute met twice, once in 1946 and once in 1947; at the second meeting it called itself the Advisory Committee on the American Institute of Biological Sciences. It recommended that the National Research Council establish the Institute within its Division of Biology and Agriculture, and that an organizing board for the proposed Institute be constituted; Nicholas became a member of that board. The American Institute of Biological Sciences was formally established in February 1948. As Chairman of the Division of Biology and Agriculture, and later as Vice Chairman, Nicholas was *ex officio* a member of the Executive Committee of the Governing Board of the Institute. When his term as Vice Chairman of the Division ended, he continued to serve on the Executive Committee of the Institute through 1955. The Institute became independent of the National Research Council in 1955, but Nicholas remained a member of its Governing Board until 1959. He also served on various AIBS committees: from 1948 until 1951 on its Committee on Selective Service; from 1949 through 1951 as Chairman of its Committee on Advisory Service to the Armed Forces; from 1951 to 1952 as Chairman of a Committee on the AIBS Roster of Biologists; from 1952 to 1954 as Chairman of the Subcommittee on Procedures of the AIBS Committee on the Handbook of Biological Data. He was the AIBS representative to the Scientific Manpower Commission until his death.

Perhaps, however, his most important administrative duties were those which grew out of his interest in the effective use of scientific manpower during World War II, and these were to accrue to the advantage not only of biologists and other scientists but of the whole nation. During World War I, it will be remembered, Nicholas had been able to volunteer for a particular service in the Medical Corps and to take advantage of his knowledge of bacteriology. During World War II and after, he was involved in the development of national policies that not only permitted the recruitment and the wise utilization of trained personnel but that also allowed scientists to be deferred from military duty when this was, in the long run, to the benefit of the nation. His sense of proportion and of the fitness of things was of great influence in the framing of such policies.

He acted as consultant or adviser to so many bodies concerned with manpower problems, and some of them, such as the National Roster of Scientific and Specialized Personnel, themselves operated under so many agencies, that here, once more, as in the case of his scientific work, it is difficult to classify his activities chronologically or systematically. He seems to have begun his work in this area, however, as the National Research Council representative on the National Roster when it was an agency administered by the National Resources Planning Board from 1940 to 1942. He continued in this capacity when the Roster was administered by the War Manpower Commission from 1942 to 1944, and when the Roster moved in 1945 to the Department of Labor, under the U.S. Employment Service, until the Roster as such became inactive in 1947. From 1953 until his death he was a member of the Scientific Manpower Commission and held a number of officerships on the Commission: the Vice Presidency in 1954, the Presidency in 1956 and 1957, membership on its Executive Committee in 1955 and again in 1962. In 1963 the U.S. Department of Labor appointed him to the National Manpower Advisory Committee's Subcommittee on Research, constituted to make comments and suggestions on the programs both of the Department of Labor and of the Department of Health, Education, and Welfare. This subcommittee met only once during the period intervening between Nicholas' appointment to it and his death.

Thus, although the Roster under its original name became inactive in 1947, Nicholas never ceased to be involved in the formulation of policies concerning personnel, and he carried on numerous other activities in this area in addition to those already specified. From about 1944 until the time of his death he was a member of the Advisory Committee to the Office of Scientific Personnel of the National Academy of Sciences–National Research Council. In 1951 another committee of the National Academy of Sciences was created to advise on scientific personnel in the armed forces; this served also as a Committee on Manpower advisory to the Office of Scientific Personnel;

Nicholas was a member of this committee from the time of its establishment until it was disbanded in 1956. In 1956 an Advisory Committee on Scientific Manpower was appointed to review and guide the activities of the Academy and the Research Council related to broad problems of scientific personnel; Nicholas served on this committee from 1956 until his death.

During World War II he also was a member of the National Committee on Physicists of the War Manpower Commission, and a member of the War Emergency Committee of the American Society of Zoologists and of the Amercian Association of Anatomists. His membership on the American Institute of Biological Sciences Committee concerned with utilization of scientific personnel has already been mentioned. Nicholas was also a member of the Selective Service committees which were created in 1948 to advise the Director of Selective Service on deferment policies following reenactment of the Selective Service Act in 1948. These committees, according to the Director of the Office of Scientific Personnel, created the concept of state committees advisory to the state directors of Selective Service; they played an important role in the development of Selective Service policies that were so important during the Korean conflict and after it, and that prevailed until the Vietnam engagement was well under way.

It is surely evident from this enumeration, long but probably incomplete even so, of the academic and professional activities in which Nicholas indulged that his wells of energy, physical and mental, were deep indeed. One of his particular flairs in life was for the enjoyment of work, and he worked with gusto. He enjoyed studying as a youngster, he enjoyed working as an adult, but throughout his life he carried on pursuits seemingly unrelated to the experiences of his work.

Some of his nonprofessional diversions were intellectual. Sundays, for clergymen's children, are not days of games and play, and Nicholas, who had learned to read early, before attending school, spent his Sundays with books when he was a child. He read avidly, and remained always a rapid and voracious reader on a wide variety of subjects.

He had been received into the Lutheran church at the age of twelve, and unlike a number of other scientists who as sons of clergymen have turned against religion itself, he always retained his religious beliefs to some degree. At the time of his death he was a member of the Board of Deacons of the Church of Christ in Yale University; the Reverend Sidney Lovett, for many years a greatly beloved University Chaplain at Yale, said of him that "in him the disciplines of Science and the insights of Religion were finely joined."

Other of his diversions and accomplishments were musical. He had an excellent ear and a beautiful bass voice. His musical education began during his third year in high school when he started piano lessons, which he continued for two years but never really enjoyed. He meantime had found an old three-quarter-sized violin, and began to fiddle. This appealed to him more; his mother drilled him, and he soon became a member of the Sunday School orchestra. She also arranged for him to have lessons from a teacher at the Harrisburg Conservatory of Music, and he eventually also played in the high school orchestra. He seems, however, to have abandoned playing the violin, and although toward the end of his life he took up the violoncello, his principal musical interests during the major part of his life were vocal. His voice changed early, and he became a member of a church choir in 1910. He continued to participate in group singing throughout his life. During his college years he sang in various college and church choirs and in the glee club. He later sang in the chapel choir at Yale and with the University Glee Club of New Haven, of which he was Vice President in 1962-1963; he was elected President for the year 1963-1964. He placed little emphasis, when he spoke of his musical activities, on his talents; singing came to him as naturally as breathing.

But for all that he could and did do, his most important talent may have been in being what he was. Mercurial, and thus stimulating, yet somehow always steadfast, he made an exceptionally strong emotional impact on those who were associated with him. Imaginative and intensely energetic as a scientist, he acted with common sense in the extrascientific world. He lived for his work, yet he lived his life, outside the laboratory as well as within it, with a particular exuberance. He had so much life, and lived it so fully, that it even now seems scarcely credible that his days have ended. Members of the National Academy of Sciences, those of his colleagues at Yale who took the full measure of his stature, those who benefited from his judgment at Yale and in the wider world, and his friends honor him in remembering him, as he did them honor by giving them so warmly and so generously of the fruits of his many labors.

Jedes Leben sei zu führen,
Wenn man sich nicht selbst vermisst;
Alles könne man verlieren,
Wenn man bliebe, was man ist.

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KEY TO ABBREVIATIONS

Am. J. Anat. = American Journal of Anatomy
Am. J. Physiol. = American Journal of Physiology
Am. Naturalist = American Naturalist
Am. Phil. Soc. Year Book = American Philosophical Society Year Book
Am. Scientist = American Scientist
Anat. Rec. = Anatomical Record
Ann. Rev. Physiol. = Annual Reviews of Physiology
J. Biol. Phot. Assoc. = Journal of the Biological Photographic Association
J. Comp. Neurol. = Journal of Comparative Neurology
J. Exp. Zool. = Journal of Experimental Zoology
Proc. Nat. Acad. Sci. = Proceedings of the National Academy of Sciences
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society for Experimental Biology and Medicine
Trans. Connecticut Acad. Arts Sci. = Transactions of the Connecticut Academy of Arts and Sciences
Yale J. Biol. Med. = Yale Journal of Biology and Medicine
Yale Sci. Mag. = Yale Scientific Magazine

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