NATIONAL ACADEMY OF SCIENCES

HERBERT SPENCER JENNINGS

1868—1947

A Biographical Memoir by

T. M. SONNEBORN

Biographical Memoir

H. S. Jennings

HERBERT SPENCER JENNINGS

April 8, 1868–April 14, 1947

BY T. M. SONNEBORN

HERBERT SPENCER JENNINGS was widely recognized and greatly respected not only as a pioneering biological investigator but also as a thinker, philosopher, and educator. He was a master of the art of setting forth simply, clearly, and vividly, in print and in public lectures, the current state of genetics and general biology and of recognizing and pointing out their implications for the general public and for specialists in various disciplines. The development of such an accompilshed and extraordinarily humane man from humble origins is a wonder worth exploring. I shall attempt to do that before surveying and assessing the accomplishments of his mature years. Fortunately, much of the story can be reconstructed from diaries, letters, and other documents in the "Jennings Collection" of the library of the American Philosophical Society. These and other sources, my own twenty-two years of association with the man, and the passage of twenty-six years since his death have provided more than the usual opportunity to study the subject and put him in perspective.

CHILDHOOD AND YOUTH (1868–1886)

The little town of Tonica, population 500, in northern Illinois, boasted three churches and no saloons during the years H. S. Jennings lived there, from his birth, April 8, 1868, to

age six, and again from ages eleven to eighteen. Tonica was the center of a small farming district inhabited by people who were on the whole practical, religious, and narrow in scope. The town's high school started just when Herbert was ready for it: he was in its first graduating class, in 1886.

A major, if not the only, center of adult intellectual life of the community was the home in which Herbert was born. His father, Dr. George Nelson Jennings (M.D., Rush Medical College, Chicago, 1864) was one of the founders, in the year Herbert was born, of the local literary society, which met at the Jennings's home. Dr. Jennings was a tremendously excited participant in this society for six years, until he took his family to California in a fruitless effort to improve his station in life.

The physician father had already risen far above the station into which he had been born (1833) in Litchfield County, in northwestern Connecticut. There he had lived until 1853, the faithful son of a poor housepainter, whose lack of drive and confidence held him in Connecticut while nearly all his relatives ventured west to Ohio or south to Georgia. Young George had labored as his father's helper and as a lone hired hand on a farm until spurred by his mother, Cindarilla Morgan, to become a district school teacher. During the years in Connecticut, his mother's family set his standards and molded his character. Uncle Ira, a liberal preacher and astute businessman, was George's model of the perfect gentleman and humane being; and Ira's son, Pliny, inspired him to smooth his rough, awkward country bumpkin ways and to aspire to self-improvement and advancement. Tales of the successes of relatives and friends who had gone to the fertile and prospering Midwest led George at twenty to shake off the bonds of his hard life and try his fortune in northern Illinois. Working at first on farms, clerking, and teaching district school, he soon saved enough to set up his parents in Illinois and, soon after, to marry Olive Taft Jenks.

Olive came from an old Rhode Island family that had settled there in 1643 and produced Joseph Jenks, Governor of the state from 1727 to 1732. Olive's grandfather had emigrated to northern Pennsylvania in 1802, and her father and mother with their eight children pushed on in 1836 to Vermilionville, Illinois. Olive was born a week after their arrival. Her family was sensitive to the main issue of the day—slavery. On the way to Illinois, they had witnessed the brutal treatment of slaves in Cincinnati. Their home in Illinois became a station on the underground railway for slaves fleeing to Canada. When she was a young woman, Olive became a district school teacher; her brother joined the Union Army.

Both Olive and George, who married in 1856, were intensely religious. Olive remained so throughout her life and devotedly supervised the religious education of her children. Even before leaving Connecticut, George had struggled with questions concerning the irrationality of some religious doctrines and of the evils perpetrated in the name of God as recounted in the Bible, but he hoped eventually to be able to recognize their "rightness." Meanwhile, he remained a practicing member of the Congregational Church and maintained religious practices at home. In deference to him, his wife temporarily left the Baptist Church and became a Congregationalist for some years.

With Olive's encouragement, George soon abandoned what to him were distasteful and unrewarding occupations, worked his way through medical school, and built up a good practice as a country doctor. Never in the least tempted to enter actively into the Civil War, he acquired the resources to collect a library and the time to indulge his love of reading and study. Soon his meditations on his readings, especially of Herbert Spencer (after whom he named his first son), Huxley, Tyndall, and Darwin (after whom he named his other son), led him to replace formal religion with science—especially evolution—as his guide to a philosophy of life. Once and for all he broke off all con-

nection with the church. To his credit and to that of his fellow townsmen, although Dr. Jennings was looked on as the village infidel, he was loved as a person and respected as a physician.

While his father was at the height of his emotional and intellectual revolution and in the midst of his peak enthusiasm for books and the new literary society, his son, Herbert Spencer Jennings, was born and grew to the age of six. It is not difficult to imagine the great influence his father had on Herbert's early development. George Jennings's autobiography records with thinly disguised pride that the child taught himself to read before he was three, read a biology book at four, preferred books on natural history at five (but Shakespeare next), and memorized many of Macaulay's "Lays of Ancient Rome." Herbert took his loved books to bed with him, not to read, but for company. Although clearly a bookish child, he also had many playmates, mostly drawn from the large clan of relatives living in Tonica. Into his play with them, he introduced the characters of the *Iliad.* When not playing with them, he preferred to be alone. In these early years were laid the foundations of the self-sufficiency that marked Herbert Jennings's life, until he found, much later, other contemporaries of his ilk.

The years from six to eleven (1874–1879) developed a very different aspect of H. S. Jennings. During this period, his father sought his fortune in California. These were years of great adventure for young Herbert—he helped to build a rough home in a deserted sandy plain south of Los Angeles; he became intimately familiar with farm animals; he traveled from Sacramento to Upper Lake, north of San Francisco, in a covered wagon; he watched hordes of Chinese working in orchards near Sacramento; he listened to the noisy, strange funeral rites of Digger Indians near Upper Lake. These and many other experiences widened the horizons of the sensitive, observant child. He started school at eight and learned with great difficulty to write. For California, with its brown hills and lofty moun-

tains, its strange trees, and many beauties, he acquired a love that persisted throughout his life. Many years later, he wrote that his idea of the most desirable life was to go to California and stay there. For his parents, the California interlude was totally different: hardship, penury, and one failure after another in farming, business, and medicine. At the end, the Jennings family was literally penniless. Herbert and the other children were more or less aware of the poverty and failures, but they were too full of adventure and fun to be appreciably affected by it.

Back in Tonica (1879–1886), the physician–father again quickly built up a good practice; but he had lost his ambition. He settled down to the quiet monotony of a country doctor's life, turning again to the world of books and thought, and finding great satisfaction and pride in the progress of his brilliant son. Herbert's mother, extraordinarily devoted to her children and active in social service, took him regularly to the Baptist Church and Sunday School, much to his silent dissatisfaction. He was an excellent student at school and a studious, persistent reader at home; but he led a happy, sociable life with his "set," which consisted mostly of his cousins, entered vigorously into their games, and enjoyed fishing and other country pleasures. Occasionally he did an odd job to earn a bit of money. This chapter of Herbert's life closed with graduation from high school in 1886.

BETWEEN HIGH SCHOOL AND UNIVERSITY (1886–1890)

Although George Jennings made a good living, it was not good enough to permit him to send his children to a university. So Herbert had to look to making a living, hopefully to save enough to further his education. Too young and inexperienced to try to compete successfully for a teaching post near home, he welcomed the opportunity, provided by the good offices of his brother-in-law, to try for a post near Laurens, in north-

western Iowa, a place too isolated and undesirable to attract much competition. Passing the two-day qualifying examination under rough and costly circumstances, he proceeded to his post in the spring of 1886 and remained at it until the end of the three-month term. He had only five or six pupils, one totally ineducable and the others little better. They were filthy and odorous as well. For the first two weeks, he boarded in the miserable home of his ineducable student, who dropped out at the end of that time. Then he boarded seven miles away in Laurens with his sister Lily and her husband, walking daily across the swampy, wild, deserted prairie to and from the school. For his $25 a month and effort at independence, Herbert Jennings paid heavily in frustration and homesickness. But he continued to study and read, devouring Gibbon's *Decline and Fall* during the noon recesses, and impressing his brother-in-law—the poorly educated but able founder, editor, and publisher of *The Laurens Sun*—as having the greatest and most wonderful mind he had ever encountered, a profound student of everything he delved into. To others he encountered, Jennings seemed frail, a poor mixer, hard to approach, and unfit for life on the frontier. He himself confessed that he kept to himself and became acquainted with hardly anyone.

As soon as possible, he returned to Tonica and, having no job, went back to high school for a year (1886–1887) of "post-graduate" work. As part of this work, he wrote an essay (a copy of which still exists) describing in detail his teaching experience in Iowa, but most of his work was in science with a new teacher, Thomas Brunk, an M.A. in botany from Cornell. Brunk was so impressed by Jennings's mental abilities and capacity to get at the root of every question that he later called him to a college teaching post in Texas. Sometime in 1886, Herbert's mother died. Curiously there is no mention of this in either his or his father's autobiography.

In the spring of 1887, Herbert again tried teaching district

school, this time in the Trout district of Illinois, near his home. Again the experience was unsatisfactory. The people of the district had little interest in education and the students were miserable, many of them in his opinion being "degenerate or on the verge." His opinion that he was not fitted for this kind of work was confirmed; he felt that, except for the money earned, teaching did more harm than good to the development of his mind and character. Again, one term was enough.

In the fall of 1887, Jennings went to the Illinois State Normal School at Normal, near Bloomington. This was a good experience. During his year there he had superior teachers, especially in mathematics, history, and the classics, and he gained much from associations with fellow students in a debating society and other activities.

This additional training, attested to by a top-grade teacher's certificate, enabled him (1888–1889) to get a post as teacher in one of the best district schools in the area, the Quaker District of Putnam County. This third attempt was completely different from his first two. The families in the district were intelligent and ambitious for their children. The children were able and included most of the top students in the county competition. Herbert made many lasting friends in Putnam County, but his work was hard and heavy. He taught everything from primer to Latin and geometry, holding twenty-seven classes a day, including sessions during recesses and noon hour, for fewer than twenty-seven students. This schedule wore him down.

So he seized an unexpected, unimaginable opportunity. His former high school teacher, Thomas Brunk, had become Professor of Botany and Horticulture at Texas A. & M. College, at College Station. In 1889 he recruited Herbert as Assistant Professor at what must have seemed a fantastic salary—$600 for the academic year, twice as high a salary as he had ever before commanded. Absurd though it seemed to hold a college post without ever having been to college, young Herbert acted then

as he always would: he grasped the opportunity and made the most of it. His duties were to help in the elementary botany class in compositae, grasses, and other forage plants, stressing their economic value for Texas ("the most disagreeable, repelling part"), and to supervise the making of gardens by students. His time was "almost entirely occupied in making indexes, lists, maps, etc., of orchards and gardens, writing letters and orders, and all kinds of miscellaneous work." Nevertheless, he managed to attend classes on horticulture, fungi, plant diseases, and plant histology and to study inorganic chemistry on his own. He also collected fungi and published his first scientific paper on the parasitic fungi of the region, in which he reported some new species.

Until near the end of the year, Jennings was unaware that Brunk was the instigator and leader of a raging academic battle that split the faculty into two bitterly opposed factions. The technical absurdity of Herbert's position as Assistant Professor, although he had never attended college, and the failure of Brunk to have given the post to another man (to whom it was alleged to have been promised) were among the targets of the anti-Brunk faction. In the end, the President, the Director of the Experiment Station, the Business Manager, Brunk, Jennings, and many others were required to resign or not be rehired. His year at A. & M. was humorously and vividly described in Jennings's last (1946) publication, "Stirring Days at A and M."

During the year, Jennings was on the whole content with his lot and suffered but little from the homesickness that had dominated his first period away from home when he was in Iowa. He kept up a voluminous correspondence with his family and friends, telling much about his work and thoughts and feelings. His plan to study Greek could not be carried out for lack of time, and he regretted slighting the "higher" subjects that were more to his taste: literature, philosophy, the Bible

(in which Ecclesiastes was his favorite book), and the ancient classics of Greece and Rome. Although he had become interested in botany (not in horticulture), Jennings wrote, nevertheless, "I would be glad to drop this all any time—be most joyful and light-hearted over it—and return again to studies which are more to my taste, more naturally. I half think I will do this yet, sometime, when I have earned enough to support me for a while. If I could think that my abilities would warrant it, that I could ever take a good place in those lines—such a place even as it seems as if I *may* be able to take in the scientific line—I certainly should do it. But it certainly would be throwing away a chance such as few men have, and I might regret it in poverty and failure all my life. It is a hard problem and one I have a great many wrestlings over."

Not until a year later would the final decision be taken, a result largely of economic opportunity, but never would Jennings's conflict of interest between science and the humanities be fully resolved.

LEHRJAHRE (1890–1897): MICHIGAN, HARVARD, JENA, AND NAPLES

Back in Tonica during the summer of 1890, Jennings read and studied in preparation for entrance into college, hoping that some day it might become possible. His father's help made it possible that fall. Herbert passed the entrance examination for the University of Michigan, receiving a year's credit toward graduation. "I was rather strongly set against scientific study and toward study of a philological nature. I had much trouble to choose my work, and could not decide definitely . . . so I made a sort of compromise and made up my mind to see a little further before decision. . . . At the end of the first semester my interest had become greatly taken up with scientific work—now for the first time properly carried on in my experience. . . . I decided to continue with it, although my interest in language

studies was unabated and I hated to give them up. . . . My interest in scientific studies continued to increase to the end of the year so that they overshadowed everything else."

It was the biology course given by Jacob Reighard, then an Assistant Professor but to be promoted to Professor the next year, that excited Jennings most. John Dewey's *Introduction to Philosophy* also had great impact on him. "Professor Dewey's attacks on Herbert Spencer's Philosophy and on Materialism showed that they had no monopoly on rigid logical thinking and partially at least set one free from my heretofore compelled adherence to such doctrines, a change which though the process was painful, as all upheavals of established principles must be, was very welcome. I was left again in the condition of suspense of judgment; the great questions were entirely reopened."

After this first year at Michigan, Jennings's financial resources were exhausted. Very tired, he went home to Tonica for the summer to recoup his energy, playing croquet and not unmindful of feminine charms, especially those of Lulu Plant, who was then being courted by his brother George Darwin. Nearly half a century later, Lulu and Herbert were to marry. As the summer drifted by, Jennings's plans for the next year failed to crystallize. He and his father lacked the resources necessary for another year at Michigan. Then, shortly before the start of the fall 1891 term, he received an offer of an assistantship in zoology. Reighard had sensed Jennings's ability and promise. His offer of an assistantship was thought by Jennings to be the turning point in his career; he returned to Michigan clearly destined to become a biologist.

He threw everything he had into his job, which proved to be very demanding. He collected the organisms needed for the class, ordered the supplies, taught the laboratory work, went over the papers and notebooks, kept the business records, and served in general as a factotum. Reighard not only set very high standards for the students, but also expected a great deal

of hard work from his assistant. Together with his own course work, including much appreciated further work with Dewey in ethics and transcendental philosophy, Jennings's duties and studies drove him to put in fourteen to fifteen hours a day, seven days a week. He wondered whether this work grind wasn't too high a price to pay for his success, especially as his poverty added the shame of shoddy clothes, shoes, ties and hats. Unlike those who claimed not to care about other people's opinions of their appearance, Jennings admitted to caring a great deal and being painfully sensitive about his own appearance. He endured his miserable state because of what he believed it could bring him in the not-too-distant future: a decent living in an intellectual occupation. He recognized that in order to reach that happy state he should perform the task in hand—no matter how hard or distasteful—with the same total commitment as if it were the ultimate goal itself.

These and other revelations of his innermost thoughts and feelings were poured out to his cousin Eva Curtis (later Page), for whom he had lifelong admiration and affection. His own sensitive nature sought and was responsive to the sensitivity of fine women. The letters of this period to Eva reveal Jennings as far more mature than the five-year-younger writer of the high school essay. His style is much more like that of his later years, and his thoughts are deep. He wrote of the responsibility of teaching, of his disbelief in individual immortality, of evolution as a relative truth, of the likelihood of free will, of the superficiality of scientific knowledge, and of the essential lack of understanding of anything in the universe, especially one's self. But of everything, he wrote with humility and uncertainty and with care to avoid upsetting the beliefs of his correspondent, who had been brought up in orthodox religion.

During the summer of 1892, Jennings became one of a small crew of rough, adventurous, uneducated men who worked for the Michigan Fish Commission. His pay of $100 plus room and

board was an important part of his family's plans, making it possible for his father to divert enough support from Herbert to enable his other son, George, to go to Michigan. Jennings's job was to preserve the fish brought in by the nets so that their stomach contents could be examined later, in order to find out how to increase the fish productivity of the inland lakes. His use of his spare time was the important part of the experience for Jennings, as it had been earlier in Texas. He used this time to study the Rotifera of the lakes. This study, continued for several summers, led directly to several publications and indirectly to his thesis research on rotifer embryology at Harvard and later to studies on the behavior, fecundity, longevity, and genetics of rotifers. The initiation of the rotifer studies was suggested by Reighard, who had proposed to Jennings that he join him in a biological survey of these lakes, taking the Rotifera as his assignment. Reighard failed to obtain funds for the enterprise, so it was temporarily abandoned; but Jennings characteristically carried out his assigned part of the plan during time not engaged in preserving fish catches.

During the year 1892–1893, Jennings continued as an assistant and graduated at the end of the college year. This was the one year that H. B. Ward was instructor at Michigan, taking the place of Reighard, who had moved up the academic ladder. There seems to have been a marked contrast in the attitudes of the new instructor and his assistant towards the students. Ward was rather high-handed with the girls in the class, while Jennings was gentle and understanding, without relaxing his insistence on high-quality performance. Naturally, Jennings's position was much appreciated.

During this year, Jennings again felt overworked and limited in scope. He yearned to break through the straightjacket of almost exclusive confinement to scientific matters. "My interest in human life, in the world as a whole—in the entire frame—was never so intense, indeed so almost consuming, when I give it a chance to come to consciousness, as it is now."

"I seem often to have good thoughts, to see occasions for action, openings for higher development; these must be dropped to take up the daily routine." "I do not know what my opinions are on matters religious or philosophical. I have thoughts on these subjects, but I have not compared them or grouped them together to see what the whole is; it is all fragmentary." "Often in conversation or otherwise I see in the character of some other person something which shows a weakness in my own thought or character: the view thus given should be definitely incorporated into my action, as it cannot be if accident be depended upon to bring it to mind." "I feel as if I need a counteraction for the harshly repressive tendencies of science." "I must try to make calls on my friends to be a more social being."

But he was less discontented with the narrowness of his concentrated study than he had been previously, and concluded that he was as content as he would be with any other single line of work. He felt as if his thinking were developing, moving forward. He began to think through his own philosophy of science, concluding tentatively that science told only *how* things worked, leaving untouched the mystery of whence, whither, and why, and that its ultimate justification was utilitarian. This movement of thought was to go much further with continued basic changes.

During the summer of 1893, Reighard's plan for the preceding summer came to fruition. Jennings and a few others (including H. B. Ward and Frank Smith) joined him in starting a biological survey of the lakes. Jennings again concentrated on the rotifers, but used his leisure to read and think about social theory, politics, and comparative religion. At this period, T. H. Huxley was his paragon of the many-sided neo-Renaissance man and greatly cheered his hopes of retaining and fostering his own bent towards many-sidedness while maintaing his enthusiasm for rotifers and their values for biological research.

Returning to Michigan for graduate work, in 1893–1894,

Jennings served as a graduate assistant, but not without some private grumbling. He felt that he was underpaid for what he was obliged to do and that his role was misrepresented. The catalogue listed Professor Reighard and Mr. Jennings as giving the course in mammalian anatomy (the cat course), but Jennings gave it virtually alone. At the time he thought this a shady procedure, and unjust. He was sorry he took on the job. He recognized Reighard as intellectually strong, an excellent lecturer, and a superb teacher of methods of scientific work, but also thought he had his own interest too much at heart and valued too little the interests of his associates. Jennings thought it had been a mistake to put his career in Reighard's hands, that for his own good he had to get away, hopefully to Harvard, to take his Ph.D. and to prepare himself "to take any kind of a place or go as high as my natural abilities would allow me." After he had arrived at Harvard, he looked back on Michigan and Reighard in a new light. At prestigious Harvard, he found none of the biologists to be "so all-around able" as Professor Reighard: "The more I see and hear of other people, the more I believe in Professor Reighard as an intellectual man." When the time came, as it would some years later, he was quite prepared to accept a position on the zoological faculty at Michigan with Reighard, who in the interim had become Director of the Laboratory (1895–1925).

It was not easy for Jennings to leave Ann Arbor after one year of graduate work. He felt very much at home there with good friends. He knew and liked the students. Classes were small (fewer than ten in the class he taught), the students serious and able. They had jolly times together, students, assistants and junior instructors intermingling freely. And Jennings was in love with one of the students, Mary Louise Burridge; by the time he was ready to leave, they were engaged. She had fascinated him from first sight with her fresh and unpredictable approach to things and continued to do so as they read, talked,

and studied together. He was happily spending most of his free time with her. It was not pleasant to look forward to separation, a separation he foresaw as lasting at least two years before he could be in a position to marry. It turned out to be four years, with very few opportunities for the couple to be together. But they did not let their intention to marry interfere with getting the best preparation for a career.

At Harvard, that was what he got. He entered as a graduate assistant in 1894 and began at once to work on a thesis under the supervision of Professor Mark. He knew what he wanted to do for a thesis before he arrived there and had been assiduously collecting material, the rotifer *Asplanchna,* hoping that Mark would let him do a thesis on its early embryology, which occurs inside the mother. Mark was agreeable. Jennings proceeded rapidly to an M.A. (1895) and Ph.D. (1896) in zoology, with minors in botany and geology.

The two years at Harvard were rich and important years in Jennings's scholarly and personal development, far more so than he had anticipated. The library, the greatest university library in America, was quickly appreciated and steadily used. The presence of able and committed graduate students with similar interests was another highly appreciated resource; the eight students (including Castle, Neal, Mayr, and Goto) in zoology seemed to Jennings a large number compared with the number at Michigan! During the second year, he and some of them (Neal, Mayr, and Goto) met informally once a week to discuss some of the great problems of biology, such as those of heredity, development, and evolution. Jennings found preparation for these discussions to be more beneficial than the meetings themselves. From his teachers he received unequal benefits. His supervisor, Professor Mark, gave him freedom and support, but not ideas. He got most benefit from two young instructors, Parker and Davenport, both only a few years his senior.

G. H. Parker's course on the nervous system and physiology of sense organs was solid, like Parker himself; and Jennings appreciated both the man and the course. Whether it had any influence in directing him to the study of behavior is not evident from available documents. These documents do tell much about the influence of Davenport and his course, Factors in Development—Morphogenesis. Jennings rented a third-floor room in the Davenport home during both his years at Cambridge. During his first semester at Harvard, he reacted strongly to Davenport's course, which gave him more ideas than any other course and set a model he was to follow in reviewing the primary sources and giving full references to them. Davenport was then a Lamarckian and an anti-Weismannian; as is well-known, he became a classical geneticist after the rediscovery of Mendelism in 1900. In the 1890s, Davenport held that heredity and development could be accounted for by action of the physico-chemical milieu. Jennings was tremendously stimulated by Davenport's point of view and by the wealth of his ideas. At first dazzled by Davenport's reductionist–Lamarckian point of view, he soon rejected it and concluded that biological discoveries merely push back a step the wonder and mystery of life without removing or explaining them.

During the summer of 1895, between his two years at Harvard, Jennings worked at the Agassiz Laboratory in Newport, Rhode Island. He credited this experience with contributing as much to his biological knowledge and understanding as did his studies at Harvard. He spent the summer observing the fantastic variety and wonder of metamorphic development in marine invertebrates. There too he shared biological exploration, living quarters, and discussion with Castle, Davenport, Montgomery, Mayr, Goto, and an earnest, bright, fine Harvard undergraduate from the Midwest, Walter Cannon. Jennings's one venture into the high society of Newport found him, as he was long to remain in such circum-

stances, ill at ease. Before returning to Harvard, he spent two weeks with his fiancée in Tecumseh, Michigan, and visited Ann Arbor, where Reighard welcomed him "as a chum," and Tonica, where the harmony of the home in which he had been reared had given way to the discord of his father's second marriage. Returning to Cambridge, he appreciated all the more its advantages and its values in remedying his rustic, midwestern, underdeveloped aspects.

Life during the two years at Harvard was a vast improvement over his previous life. The first year, he had an assistantship (remission of the $150 tuition plus $225), which permitted only stringent living conditions and not nearly enough exposure to the cultural life of Boston; but the duties were light—he taught three days a week from 9 to 4:30 and in only one semester. So he had time for courses, research, reading, thinking, and letter-writing. His qualities of mind, character, and research were quickly and greatly appreciated. He became the candidate of the Zoology Department for a coveted Morgan Fellowship for his second year and won it. The fellowship, with its stipend of $500 and no duties, freed him entirely for study, research, reflection, and as much as he could afford of Boston's cultural life. Although he complained of the exorbitant minimal admission fees ($1), Jennings indulged in opera, symphony concerts, chorals, Shakespearean theatre, and even the cheaper (25-cent admission) Gilbert and Sullivan performances.

The tangible recognition represented by the fellowship raised his spirits and self-confidence. He admitted to a few intimates his feeling that he was beginning to be a master of biology and that he would be prepared to deserve and handle any available college position. The world seemed much brighter, and he was rarely depressed. He developed an appreciation of the wisdom of the relaxed pace at Harvard—the attitude that an educated, cultured person sets aside time from work to enjoy many facets of life. He abjured his previous

unduly long workday (which in truth he had never expected to maintain after it had won him the opportunities he believed it would); set aside some time daily for recreation and the "second life" of culture, people, and nature; and learned to heed the first signs of overwork, convinced that he could accomplish as much in less time when fit. Applying these principles, his health improved, except for an attack of mumps, and for the first time in his adult life he began to exceed his previous 125-pound limit.

Most of what is known about Jennings at Harvard comes from letters. Those to his fiancée have disappeared, but S. W. Geiser preserved copies of many letters written to his father, his brother George, his sisters Aldie and Kate, a friend, Joseph Brennemann (his younger roommate at Michigan, who came from the countryside near Tonica and became a pediatrician), and his cousin, Eva Curtis Page. The letters to Eva reveal his thoughts on religion, biology, and philosophy, and show that he was preparing his character and conduct for marriage as well as for a professional career. He envisioned a modest home, as happy as the home of his fiancée's parents, as artistic as his fiancée's taste and talents; and a couple, free of monetary worry, with time to enjoy life together with mutual attention and consideration, and to share things large and small.

The letters to his father and sisters provide the first available evidence of his talent for popular exposition of scientific observation and thought. At this he was already a master, like his idol Huxley. Davenport's ideas were beautifully explained by his pupil, with homely, telling similes and were related to the Lamarckian–Weismannian antithesis; Jennings's own embryological observations at Newport were spun like a yarn of the Arabian Nights. His thesis, as an example of basic research, was likened to artistic endeavor in the sense of being an ideal, spiritual, nonpractical attempt to discover and represent truth, seeking the general in a concrete, isolated example.

Jennings's thesis on the early embryology of the rotifer, *Asplanchna,* was not only a meticulously carried out (he claimed, "more minutely than has ever been done") and thoroughly documented study of cell division and cleavage, but also, in typical Jennings fashion, a searching discussion of the significance of his findings in relation to current "laws" and theories of cell division and early development. He submitted his thesis to compete for the Walker Prizes of the Boston Society of Natural History and it won their first prize ($60). He competed for Harvard's Parker Travelling Fellowship ($500) and won that. This enabled him to spend a year in Europe, the last of his *Lehrjahre* (1896–1897), instead of accepting a one-year appointment as instructor at Indiana University or waiting for a vacancy in the instructorship at Michigan, which didn't materialize anyway. Before setting forth for Europe, he made a long visit to his ailing fiancée in Tecumseh.

Plans for work in Europe were not fully settled until after he went abroad. An important part of Jennings's plan was to learn German, which he began at once in a Harz Mountain pension recommended by Parker, and to absorb German culture, especially its music. He had been attracted to music from his earliest youth and had been surprised to note in Boston what a large part music played in the life of cultured people. There he became a Wagner enthusiast. Little wonder then that music ranked high in his plans for life in Germany. So he tramped through the mountains and woods, visited the sights, and took in the music.

The scientific plans, still tentative, were contingent on being located in a cultural center. He knew he did not want to continue in purely descriptive biology, which he thought had landed "biology in a sort of Dismal Swamp." Experimental physiology and the *Entwicklungsmechanik* of Roux and Driesch, which he had learned and thought about in Davenport's course, seemed "a great change for the better." Working with Roux

was ruled out because of the cultural limitations of Halle, the town in which he was located. He wrote to several other people exploring possibilities and settled on Verworn, at Jena, after receiving from him a warm response.

This proved to be one of the most felicitous decisions of Jennings's life, far more so than he imagined at the time it was made. He looked on his forthcoming studies as a new and original way of extending the descriptive embryology of his thesis into the experimental domain. To obtain understanding of the factors governing the movement of cells during early embryology, he imagined much might be learned by studying the factors governing the behavior of isolated cells, *i.e.*, their reactions to stimuli. Verworn had been successfully studying the reactions of individual cells to such stimuli as the electric current; so Jennings proposed to extend these studies to other stimuli. As events were to show, this rationale for experimental embryology was more appealing in imagination than fruitful in actuality. Jennings did not learn anything significant about the behavior of embryonic cells from this approach. Instead, he became fascinated by cell reactions to stimuli as a subject in itself and as a basis for comparative invertebrate psychology. The work done in Verworn's laboratory was in fact the beginning of his most successful and important work as an experimental biologist.

Verworn, only five years older than Jennings, called his attention to the fact that the cell he worked on—the ciliated protozoan, *Paramecium*—oriented and swam toward the cathode in an electric current when it was already swimming, but failed to respond in this way, and seemed not to respond at all, if it was quietly in contact with a solid object when the current was turned on. This was the starting point of Jennings's investigation. He resolved to examine the responses of *Paramecium* to solid objects, gravity, chemicals, and to combinations of these stimuli with each other and with the electric current. A

few months after he started work, he wrote: "I've been discovering some queer Paramecium tricks in the last few days. I'm beginning to believe that one might as well stand off and watch a city full of men, with a telescope, and make theories about the forces which compel them to move in such and such a direction or stop moving at certain times. However, all I want to find out is what there is in all this 'reaction to stimuli,' etc.; I don't care how it turns out." The results of his work during the one semester at Jena, as sole experimentalist in the laboratory, were written up and published as the first of a series of papers on "Studies of reactions to stimuli in unicellular organisms." He reported in this first paper the aggregation of paramecia in weak acids and the mechanism of this aggregation, their negative reaction to alkali, their nonreaction to certain chemicals and to osmotic pressure, the responses to certain combinations of stimuli, and many other basic observations.

While in Jena, Jennings attended lectures by Verworn on general physiology, by Biedermann on human physiology, by Liebmann on psychology, and a few by Haeckel. (He also attended a club of American students devoted to pedagogy and philosophy.) Haeckel seemed to him "too popular and commonplace" to be worth continuing; Liebmann, a Kantian, he found to be the most impressive lecturer he had ever heard; Verworn was largely a repetition of Davenport, less deep and broad, but brilliant and solid. Verworn seemed an all-around good man of uncommon powers with a strong philosophical bent, looking on science as the investigation of the laws governing the only reality—man's mental phenomena. Verworn thus denied materialism—the existence of an objective material world—but also denied vitalism. On all this, Jennings formed his own opinions and continued to develop them for many years thereafter.

From Jena, he went to Italy, again being first an avid tourist, ecstatic over the art and music, before settling down to

work at the Naples Zoological Laboratory. There he made some unsuccessful attempts to do embryological work of the sort made famous by Roux and Driesch and their schools. At the same time he gave much thought to the great problems of biology and their current status, these reflections serving as a basic frame of reference for all of his subsequent work and thought. And he made his first contact with some of the leading European biologists. Driesch, impressed with Jennings's thesis on *Asplanchna,* had written a laudatory review of it for the *Archiv für Entwicklungsmechanik* and called on Jennings to show him the manuscript. Thus began most cordially a relationship that was to turn much later into one of profound disagreement on vitalism and "psychic research." Jennings also became acquainted with Herbst, Zur Strassen, Haecker, Ziegler, Richard Hertwig, Waldeyer, His, and many others.

As Jennings's year in Europe drew to an end, plans for the next year had to be made. Reighard and Mark urged him strongly to stay for a second year. He applied for a renewal of the Parker Fellowship and doubtless would have obtained it. But he decided against this and withdrew his application because he was miserable at being so long delayed from marriage and kept so far away from his fiancée, whose life was then shadowed with the sorrow and stress of her father's long illness and death. The decision having been made, Jennings began to worry about his chances of finding the kind of position he desired. He feared that his failure to follow the advice of Mark and Reighard might lessen their support, but this fear was totally unfounded. There was more substance to his worry about a glutted job market. He wrote to his friend, Frank Smith, who had been a colleague in the work of the biological survey and had settled into a good secure position at the University of Illinois, "Zoologists are getting terribly frequent nowadays and it makes me speculate about the future." The competition was getting rough. Visible men on the spot had a

great advantage over the invisible man thousands of miles away in Italy. In spite of excellent credentials and favorable reactions, Jennings could not get a bid sight unseen. So he returned to the States early in the summer of 1897, but too late to secure any of the better opportunities. The best he could get was an instructorship in botany and bacteriology at Montana State College, in Bozeman, the lesser of the two offers that had been made to his Harvard fellow student, Neal, who had been his comrade in Italy and had wisely come home earlier.

DESCENT AND RISE (1897–1907): MONTANA, DARTMOUTH, MICHIGAN, NAPLES, PENNSYLVANIA, JOHNS HOPKINS

The salary ($900) at Montana was not bad, being on a par with what Michigan was paying for a new instructor; but the institution was remote, its physical condition was pitiful, the assignment was outside Jennings's field of special competence, and he had virtually no opportunity to continue his researches. In every realistic sense he had fallen from the crest of the wave to the bottom of the trough and again had to face the task of working his way up.

Naturally, he was discouraged. His fiancée's illness continued to prevent her return to college. Her spirits (and his) were further depressed by the illness and death of her father, followed quickly by her mother's emergency operation for an advanced cancer, detected almost too late. She nursed her mother during her complete recovery, keeping house without help for the family of four. The prospect of leaving home to marry was not bright; and, even if it had been possible, Jennings was three days away in a job far beneath his expectations and capacities. But these were two courageous souls not to be long diverted or subdued by adversity.

Not yet thirty, Jennings enjoyed excellent health and the character to make the most of his opportunities, however short of his desserts they might be. The assignment in botany and

bacteriology was seized as an opportunity to learn, as well as to make a living. The lack of office or lab space, the poor buildings and apparatus, were not used as an excuse, but as a reason to work and plan for better conditions. Part of his teaching was done in a twelve-foot-square room in the high school, part in an old skating rink "metamorphosed by partitions into an 'Academy'." Both rooms housed other classes as well, so Jennings had no place to call his own where he might work between classes. But, he said, "we are struggling on, all of us in the same fix, and all cheered by the possibility and hope that *some* time we shall have a college building and every professor have a room of his own."

A new building was in fact under slow and much delayed construction. In anticipation of the move, Jennings had been authorized to order apparatus and reagents; he did so to the tune of $600. Meanwhile, he made do with little more than microscopes, by finding favorable organisms and stages of their life cycle for his classes. He had one student in economic botany, six interested and hard working students in cryptogamic botany, and sixteen in phanerogamic botany. He realized, more than ever before, "how problems of the two sciences (botany and zoology) are exactly the same." He described bacteriology, to which he came almost completely unprepared, as "a very interesting field and I'm glad to have a chance to work it up to some extent. . . . The whole year will be valuable to me—if only I can switch over into something else later." Indeed, time was to prove its value; it provided the foundation for Jennings's capacity to take the then unusual and important step of including unicellular plants and bacteria in his broad and comprehensive review, "Genetics of the Protozoa," which would be published thirty years later.

With characteristic energy and thoroughness, he threw himself also into his additional assignment as botanist at the Agricultural Experiment Station, attending various agricultural and

horticultural meetings, work for which he nevertheless did not feel fitted. He also had full responsibility for the chaotic herbarium, which he put into good shape, classifying the specimens and making them usable. His ambition was to leave the herbarium as a memento of his presence in Bozeman. He gave talks to the Faculty Club, a Domestic Science Club, and elsewhere in the state on experimental biology, bacteriology, and heredity. And on top of it all, he tried desperately to find some time to continue his behavior work on *Paramecium:* "My only chance now is not to let myself be entirely forgotten. Having gotten completely outside of real scientific circles and even out of zoology, I'm afraid it will be difficult to get back." If he did any research, it did not come to publication that year. Withal, he found time to read Kant and Schopenhauer, critically garnering the wheat from the chaff, and entertained himself in the evenings with the stories and novels of Stevenson, Thackeray, and the like.

During the Christmas holidays, he made the long trek to Michigan to be with his fiancée for a few days. "It seemed like a sort of crazy thing to do, from such a distance—but we live only once, and these things are measured by a very different standard on the inside from on the outside."

Soon he began to look to possibilities in the East (Ohio State, Michigan, Dartmouth) for the next year. By late March, Jennings had settled on a fine one-year position ($1400) at Dartmouth, where he would take the place of Gerould, who was to be in Europe. This he considered "a good place to get a position *from.*" He also arranged with Reighard to join in the summer survey of Lake Erie for the U.S. Fish Commission.

That he left behind him at Montana a tremendous impression on colleagues and students is abundantly attested to in letters collected in 1934 by his biographer, S. W. Geiser. He did not lower his standards for students and made only one concession to their weak background preparation: He gave them

perhaps more sympathetic attention and inspiration than otherwise, if that were possible. In doing so he was not in the least supercilious or condescending; that was utterly foreign to his character. As always, Jennings made the best of his situation.

The year at Montana ended and he headed for Michigan, where at last he married his long-time fiancée, the artist Mary Louise Burridge of Tecumseh, on June 18, 1898. The happy couple went to Put-in-Bay, Ohio, an island serving as the summer survey headquarters. Arriving well before the survey party, they had the place alone for their honeymoon. Three weeks after the great event so long looked forward to, Jennings wrote his closest friend, "There isn't any disenchantment nor the slightest indication of one, in marriage, and I feel now that I am sure there's to be none." The Jenningses spent their time boating, walking, sitting on the rocks, reading aloud the *Iliad* and the *Odyssey,* and making a map of the distribution of the twenty-five water plants in one arm of the lake, fascinated as earlier by survey work.

The survey had already been delayed two weeks from the proposed starting time; as Jennings wrote, the remaining six weeks could hardly permit much accomplishment. Besides, he was worried about his brother, George, who was in the thick of the Spanish–American War in Cuba. But the work had to be done. As he wrote, "Competition is fierce, and if I don't keep moving I am going to be left." He did move; no less than three research papers based on the work of those six weeks appeared in 1899. They were papers II, III, and IV in his series, "Studies on the reactions to stimuli in unicellular organisms." His work on *Paramecium* in Verworn's laboratory had shifted his focus from rotifers to Protozoa, from morphology and distribution to behavior; so during this summer at Put-in-Bay he concentrated on the Protozoa, which, in earlier years of the survey, had been assigned to others, first Frank Smith and later C. A. Kofoid.

After this happy and successful summer, Jennings went on to his post at Dartmouth light of heart and full of hope. He was indeed back in the swim of things again. He prepared for publication papers based on the work of the summer and a more general summary paper, "The Psychology of a Protozoan," for a psychological journal. Viewing the reactions of Protozoa as "the beginnings of mind," he continued for years to call the attention of psychologists to his findings. While at Dartmouth, he also completed a monograph on the rotifers of the United States (1900), the drawings for which were made by his wife. On the march again, he "walked with breathless haste," according to the laboratory director, Professor Patten. The following year, Dartmouth offered him a position in botany, and Michigan an instructorship in zoology. He accepted the offer from Michigan, his first opportunity to stay on in a position in his own field of work.

An important event of Jennings's year at Dartmouth was the contact made with Raymond Pearl, with whose life he was to be intertwined in various ways for more than fifty years. Pearl was then a senior undergraduate. Earlier, he had switched from classics to biology after one week in the required course on elementary biology given by Professor Gerould. When Jennings arrived to give Gerould's course, Pearl served as his assistant. The two men had much in common: zest for biology, intense interest in the classics and literature, devotion to music, and a broad inclusive interest in the whole universe. Pearl was strongly attracted to Jennings. He went with him to Michigan as his graduate student, doing his Ph.D. thesis on the behavior of planarians, and participating during each of his three summers at Michigan in the survey work on the lakes. When the Jenningses left Michigan, the Pearls took their house. When Jennings left the University of Pennsylvania for Johns Hopkins, Pearl took his place.

The relative positions of the two men then reversed. Pearl

took the lead in developing statistical and mathematical biology; he worked closely for a while with Karl Pearson in London. Jennings later followed Pearl's lead in these fields and made important contributions to them. Pearl also took the lead in applying statistical techniques to a study of conjugating paramecia; he thereby raised the question of assortative mating, *i.e.,* a tendency of like to mate with like. Jennings then made comparable and decisive studies of the subject. During World War I, Pearl was head of the Statistical Division of the Food Administration in Washington, D.C., under Herbert Hoover; and Jennings was a member of Pearl's staff, assigned to the statistics of sugar supply, needs, and distribution.

In 1918, Pearl followed Jennings to Johns Hopkins, but to a part of the university five miles distant—the new School of Hygiene and Public Health. Seven years later, when Jennings was trying to get support from the Rockefeller Foundation for work of his department, Pearl succeeded in obtaining from them magnificent support for five years to set up for himself at Johns Hopkins an independent Institute for Biological Research. Jennings's hopes were dashed. However, at the end of this five years, the Rockefeller Foundation ceased to support Pearl's institute and it came to an end. In the same year, Rockefeller began a modest continuing grant to Jennings in support of his research.

Like as they were in the nature and breadth of their interests, Pearl and Jennings were at opposite poles in personality. Totally unlike Jennings, Pearl was aggressive, positive, partisan, highly (and it seems happily) controversial, exuding self-confidence and authority. To close the book on the relations between these two giants, after Pearl died in 1941, Jennings wrote (1943) a long, fully appreciative, generous, and sympathetic biographical memoir of him for the National Academy of Sciences.

Pearl was not the only person to be involved in changing relations with Jennings. Another was H. B. Ward. During

one of his student years at Michigan, Jennings was Ward's laboratory assistant. In 1902, Jennings was Director of the Survey of the Great Lakes, while Ward was a member of his staff. Less dramatic was Jennings's shift with Mark. Mark was the supervisor of Jennings's Ph.D. thesis work at Harvard. In the summer of 1906, Mark and Jennings served as equals in a trio (the third being E. B. Wilson of Columbia) of top-level advisors to the University of California in regard to the establishment of an oceanographic branch at La Jolla. Of this, Jennings wrote: "It seems remarkable to be made one of a trio with these two."

Part of Jennings's commitment at Michigan was to write a book on the anatomy of the cat, begun as a set of laboratory directions by Reighard. This he completed during his first year at Michigan (1899–1900). Again his work included drawings by his wife, for which she received $400. The Reighard and Jennings *Anatomy of the Cat* remains to this day the standard text on the subject; for many years, it yielded Jennings modest royalties.

The first year at Michigan was a good year. Although he didn't receive a grand salary, Jennings had the precious gold of time to do research. Both of the graduate students in zoology elected to work with him, and his scientific output again began to zoom. He had to give only one lecture a week for the hundred students in the introductory biology course and an hour or two a day in the class laboratory, which was looked after by five assistants. Jennings himself went over the students' notebooks and had the responsibility for all purchases and for keeping the accounts of the whole department. A few months after arriving at Michigan, Jennings was already being sounded out by "a good university" for an assistant professorship to start a Department of General Physiology, but this came to naught. Financially strapped, he thought of trying to add to his income by writing a textbook on introductory biology and started work on it.

At the end of the first year at Michigan, feeling relatively

secure, the Jenningses made the decision to splurge on a delayed "wedding trip" to Europe. Landing in Holland, they traveled up the Rhine and on to Switzerland and Italy. Although their activities were limited by the recurring illness of Mrs. Jennings, the summer was a great antidote to the hard work of the preceding three years. Jennings's sense of time and values kept his balance of interests and activities, if not his bank balance, during these years of stringent finances. He never forgot that he had only one life to live and should make the most of it; and he always strove not to let his scientific interests and ambitions deprive him of broader interests and time to share them with his wife. Only when fighting for survival and a push ahead did he let himself temporarily neglect broader interests.

When he returned to Michigan in the fall (1900), after the delights of Europe, Jennings's funds were so low that for a long time he had to draw his salary a month in advance to pay current expenses. Seeing no chance for advancement in salary or rank unless an offer came from elsewhere, he kept looking. His failure to rise at the time was not due to lack of effort on Reighard's part. He considered Jennings to be "without an intellectual superior" in American biology and encouraged and supported him in every way he could—allocating him everything he wanted in the biology building then being planned, assigning him minimal teaching duties, and giving him all the apparatus he requested.

At this time, Jennings encountered, and was long to be plagued by, opposition to his research claims, since his behavior work ran afoul of the views and reports of one of the foremost biologists in America—Jacques Loeb, and his student, Garrey. This conflict is worth examining as an example of a basic schizophrenia that has plagued biology for centuries: the split between those who see life as solely physico-chemical, *i.e.,* the reductionists, and those who see life as a new level of complexity far above the simply or solely physico-chemical. Jennings had

begun to crystallize his position as a student at Harvard when he recoiled from the simplistic reductionist teachings of Davenport. In his first experiments on the behavior of *Paramecium,* while still at Jena, he had been almost overwhelmed by the complexity of the behavior of this "simple" cell. As his studies continued in subsequent years, he showed that the responses of the cell were a function of its *gross* structure, important aspects of which were the cell's asymmetry and correlated spiral movement. Similar results were obtained on various unicellular and multicellular organisms. They could not be understood as simple physico-chemical materials, but only as complex arrangements of such materials into a higher level of organic structure that had new properties and modes of fuctioning.

For centuries, as again today, there have been recurrent efforts by the most "advanced" biologists to make biology a "hard" science, *i.e.,* physico-chemical. In the first decades of the twentieth century, Loeb was greatly admired as a leader who pushed biology in that direction. Trained primarily in physics and chemistry and, in important respects, innocent of biology—like the current generation of most "advanced" biologists—the Loeb school believed it could be shown that the behavior of cells was in fact simply a system of physico-chemical reactions; and, what was worse for Jennings, they reported their failures to confirm his results in their attempts to repeat his experiments. So they attacked Jennings viciously in their papers and thought of him as a "vitalist," *i.e.,* one who resorted to a nonmaterial vital force of an essentially nonscientific nature. This was a total misunderstanding of his position.

Jennings seized opportunities to meet with Loeb and to try to clarify his position, to explain how he had been misunderstood, and to pinpoint reasons for their disagreements in experimental results. He appreciated the importance and value of Loeb's efforts to stress physico-chemical aspects of biology, but found him surprisingly ignorant of some critical aspects of

the cells, especially their asymmetry. The personal encounters between the two were cordial and pleasant, but the publications of Jennings's opponents, especially Garrey, remained unaltered in tone. Finally, at the Christmas meeting of the AAAS, Jennings performed under a microscope the experiment that Garrey had claimed couldn't be repeated, the whole experiment being projected through the microscope onto a large screen for all to see. He also repeated the whole show privately for Loeb, who said he was now convinced that Jennings had been right all along and that he would tell Garrey to correct his statements in his next paper. Interestingly, in his presentation at the meeting Jennings did not mention the names of those who had been denying the validity of his experiments. To his friend Neal he wrote: "I . . . didn't give Garrey the general blowing up that I had come loaded for. It would have been the easiest thing in the world, as his paper is a fearful thing,—full of errors of the most fundamental nature, that positively vitiate the whole thing and I was in a position to demonstrate this with the stereopticon, but refrained. It's a good thing anyway to have this in reserve, for Loeb they say isn't to be depended on, and may later go back to his old attitude even after admitting what he did. But he certainly treated me finely, and I enjoyed being with him very much. He showed though that he doesn't know anything about this particular matter and isn't competent to work on it or talk about it at all: many of his ideas were positively comical, in view of the facts." So Jennings went about his business, giving similar demonstrations and lectures to Davenport's class at the University of Chicago and elsewhere. He was justifiably confident of the correctness of his work and chose to show the evidence instead of using merely argument or invective to make his points.

Meanwhile, things got worse for Jennings at Michigan. Early in 1901, Reighard had a recurrence of the breakdown he had experienced some years before, and had to enter a sani-

tarium. Jennings, in addition to his regular duties—a new course in general physiology and supervising four research students—gave the lectures for Reighard's comparative anatomy and cat courses. He had no time for research. And he was still at the bottom of the academic ladder, an Instructor at $1200, still borrowing his salary a month in advance. He was discouraged and tried to get some inspiration by reading biographies of successful scientists—Huxley, Kölliker, and Pasteur. To Neal he wrote: "I have been getting somewhat discouraged over science, living along thus, drawing my salary in advance with no prospect of advancement nor doing the things that it is nearest my heart to do. I sometimes speculate on whether it is too late to turn to something else, where a man would have a chance of becoming more nearly free: I'm afraid it is." He would never have believed that six years later he would be a full Professor at a top university with most of his time free for research.

Happily, an outside offer came in the spring of 1901. A Detroit newspaper recorded the threatened exodus of one of Michigan's best men, saved only at the last moment by promotion to Assistant Professor and an increase of salary to $1600. Jennings also was temporarily given Reighard's place as Acting Director of the survey of the lakes for the summer of 1901. This he didn't enjoy, because it left him no time for research and because, as he wrote to Neal, "Management of men and affairs, official correspondence, and the like, is unaccustomed work for me, and not that for which I was especially designed." Yet he was to do just that for nearly thirty years. After another busy and fruitful year at Michigan (1901–1902), he was appointed Director of the lake survey for the summer of 1902, his last stint with the survey.

Still mired in money problems, Jennings pushed ahead during the academic year 1902–1903 on the proposed potboiler, the textbook of introductory biology. He finished the writing and

Mrs. Jennings was working on the illustrations. They were still not finished four months later. Whether the illustrations were ever finished or, indeed, whether the book was ever submitted for publication, I have been unable to discover. In any case, the Jenningses' energies were soon directed to a new adventure, one of the happiest of their lives.

It came about in this way. The Carnegie Institution of Washington had sought Jennings's advice on how they might best spend institution money. He advised them to use it to free good men (not mentioning himself) of other duties so they could have time for research. Carnegie responded with a grant of $250 to Jennings to aid his investigations. (He needed the money for apparatus, reagents, typing, and drawing.) Soon thereafter, the institution made him a grant of $1000 toward a research table and expenses for a year at the Naples Zoological Laboratory. Then, in June 1903, Jennings's father died, leaving financial problems that put some temporary strain on the son. To make a go of the Naples venture, he earned an extra $100 teaching for Reighard a new course on experimental embryology and $240 teaching summer school at Michigan. His total wealth at this time was about $600. With the Carnegie grant, he thought he could manage a year in Italy.

During the spring and summer of 1903, while preparing for the year in Naples as Research Assistant of the Carnegie Institution, the long wished for outside offer was being negotiated. Professor Conklin, then Head of Zoology at the University of Pennsylvania, offered him an instructorship at $1750. Jennings, already Assistant Professor at Michigan, held out for the same rank and for a leave of absence the first year so that he could go to Naples. Conklin agreed. Reighard tried hard to keep Jennings at Michigan and personally pled for this before the regents, but the university had sunk its funds for biology in a new building and the regents could not allocate anything for a salary increase. So in August, the Jenningses left Ann Arbor for

good and looked over Philadelphia on their way to the steamboat.

The year at Naples was both delightful and exceedingly productive. Their joint diary records the couple's daily life, their work and play, their ills and joys, their impressions of people and sights and events. They made many new and lasting friends at the Naples Laboratory, including Hans Spemann and the protozoologist Penard. Their capacities for broad enjoyment of the world now had the chance for exercise that had heretofore been largely stifled by hard, narrow work except for the summer of 1900 in Europe. Jennings not only pushed his research on behavior considerably further, but also wrote seven research papers summarizing in logical order his work and thought on the topic. These papers were published as a book, *Contributions to the Study of the Behavior of Lower Organisms.* (Publication #16 of the Carnegie Institution of Washington, 1904). While still in Italy, Jennings was approached by Whitman of the University of Chicago in regard to filling the post left vacant by Davenport's departure. Matters moved so slowly during the summer of 1904 that Whitman decided it would be unethical to bring them to a head so close to the beginning of Jennings's engagement at Pennsylvania. This decision relieved Jennings, especially since Whitman promised to renew negotiations later.

At the end of this great year, the Jenningses returned to the United States and set up shop in Philadelphia. A few months after he started, Chicago made him the promised offer of $2500 for the next academic year, but the Jenningses agreed to stay at Pennsylvania for $2250. They loved Philadelphia, their association with the Conklins, and the cultural opportunities of the city. Mrs. Jennings studied drawing and painting at the Academy of Art. Jennings taught only two advanced courses, on general physiology and animal behavior. The buildings and equipment were poor; quarters were cramped; "but after all,

those aren't the chief things in life. I think associations with pleasant and interesting colleagues is the best thing, and that I have here."

The years at Pennsylvania (1904–1906) were years of intense activity for Jennings. His behavior work had become widely appreciated and he was in demand to give outside lectures. Several, given once per week, on "The Beginnings of Mind," at the Brooklyn Institute of the Museum of Arts and Sciences, were particularly wearing—he started back to Philadelphia at midnight after each lecture. During the spring of 1905, his health began to decline. He lost considerable weight, which he could ill afford; his digestion was badly upset; he had a succession of severe colds; he developed a mild case of albumenuria; and his appendix began to cause trouble. On examination for life insurance, he was refused. So he was shocked into taking it easy during the summer of 1905. Although only thirty-seven, he wrote, "I can't work so steadily as I used to, and it looks as if I can't expect to do any more than my college work and keep well."

He spent June at the Tortugas Laboratory which was run by his old friend, Mayr, from the summer at Newport, and there met Professor Brooks, famous researcher and biological philosopher and Director of the Zoological Laboratory of the Johns Hopkins University, who was soon to play a major role in his life. Brooks had been a referee of Jennings's manuscript for the Carnegie book on behavior and was much impressed by it; but of this Jennings knew nothing. The rest of that summer was spent at Woods Hole, Massachusetts. This was Jennings's first visit to this great summer gathering of biologists. There he gave several lectures and continued work on another book, *The Behavior of Lower Organisms,* but at a pace that permitted him rapidly to regain lost weight and recover his health. Of this health episode he wrote: "I am thoroughly convinced that continued immurement in a brick house in a city, along with a

good quantity of college work, would finish me up within a limited period. There has seemed some prospect that I might get out of college work, into a pure research position with the Carnegie Institution. That would allow us to arrange life on a proper basis—live long and be happy, and get some good work done, too!" Such an offer never came; Jennings went on till his retirement "with a good quantity of college work." From this time on, he was to fight repeatedly the battle of trying to regulate his life so as to keep well and still do scholarly work.

The recuperation during that outdoor summer at Woods Hole, where he lived in a tent, encouraged him to commit himself heavily for the coming year. Professor E. B. Wilson invited him to give the lectures in the Visiting Biological Lecturer Series at Columbia and to have his new book published by the Columbia University Press. He accepted, raised about $1000 for the publication of the book, hopefully to be recouped by receipt of two-thirds of the sale price of each copy sold, and gave a series of five lectures at Columbia in February 1906.

These lectures were repeated in the same month at the Women's College of Baltimore (later Goucher College) at the invitation of Professor Maynard M. Metcalf. A particularly interested member of the audience was Professor Brooks, who, as mentioned earlier, had his eye on Jennings as one of the up-and-coming young biologists. He invited Jennings to lecture to a joint meeting of his department with the Department of Psychology and Philosophy, presided over by the distinguished Professor J. Mark Baldwin. The lecture garnered Jennings an offer to come to Johns Hopkins as Associate Professor of Experimental Zoology, salary $3000, with the promise of succeeding Brooks as Director when Brooks retired. In his diary, Jennings wrote: "This astonished me extremely; it seemed impossible. But following the maxim that one should accept his opportunities, I accepted." But not without hesitation at leaving his beloved Philadelphia.

Before going to Baltimore, Jennings used the excuse of the visit to La Jolla with Mark and Wilson to spend the summer in California. He and his wife were entertained by the wealthy Scripps family and had joyous times with some of their own relatives, especially his sister Aldie and his brother George. In his diary he wrote of George's wife, the former Lulu Plant, whom he had admired as a youth in Tonica, that she was "as charming as ever." The California visit brought back memories of his childhood. He visited Artesia, where thirty-two years earlier his father and uncle had tried to farm until the water failed them, and the nearby schoolhouse, where he had begun his schooling exactly thirty years earlier. He and his sister relived their early years in going over the papers, including the remarkable autobiography of their physician father, who had died in California just three years before. Jennings also found time to carry out an investigation of the modifiability of the behavior of the starfish, his last research on behavior before changing fields. On this and his other behavior work, he gave greatly admired lectures at La Jolla, San Diego, Berkeley, and Chicago before settling in Baltimore just before the fall term of 1906.

Jennings's experimental research, until the call to Johns Hopkins, was all conducted on the reactions of lower organisms to stimuli. From the start at Jena ten years earlier, he had had the insight to recognize the bearing of his work on psychology and he took and made occasions to drive this important point home. Previously, the two fields were largely pursued independently without much mutual awareness. His efforts to overcome this isolation were outstandingly successful. The leading behaviorist of the day, John Watson, attended Jennings's lectures at Johns Hopkins and was clearly influenced by him. Jennings's book, *The Behavior of Lower Organisms,* was repeatedly reprinted, most recently by Indiana University Press in 1962, fifty-six years after the first printing. In the preface

to this reprinting, another psychologist, Donald D. Jensen, wrote that the book remains "a basic text for the student of animal behavior . . . a work . . . important in the history of experimental psychology." No subsequent researches by Jennings exceeded in importance and lasting effect on science those he carried out on behavior in the first decade of his research career.

Starting work at Johns Hopkins in the fall of 1906, Jennings was promoted in 1907 to Professor of Experimental Zoology. He wrote to his old friend Neal: "And so I have finally come to man's estate in my profession! Eight hours of teaching per week for four months: the rest of the time for research! I never expected to find such a place: indeed, I wouldn't have believed such a one to exist in American universities! I had a chance to go back to the University of Pennsylvania on this same footing of work, rank and salary and was much tempted to do it. . . . The men in this department here are geniuses, but eccentric, which doesn't make the social side as attractive as at Philadelphia." But he stayed at Johns Hopkins for thirty-two years, until he retired in 1938.

A few years after Jennings's arrival at Johns Hopkins, Brooks, the Director of the Laboratory, died. President Gilman appointed a committee to recommend a successor. The committee recommended T. H. Morgan of Columbia, then at the start of the great period of his work that established the chromosomal and gene theories of heredity. No one could find fault with this choice—except Jennings. When he got wind of the committee's decision, he confronted President Gilman with the letter that set forth the terms on which he had come to Johns Hopkins. One of the terms was that he was to succeed Brooks on the latter's retirement. Gilman had no recollection of the agreement, but he stood by his word. So Jennings became Henry Walters Professor and Director of the Zoological Laboratory in 1910. He had indeed reached the top at the age of forty-

two. And he learned a lesson: have all agreements in writing. That lesson he never forgot. He put all of his own agreements in writing, spelling them out in full. I know, because when I became his research assistant in 1930, he wrote me a letter stipulating every aspect of my duties. This hurt my feelings and I told him that there was no need for such a letter, that he should know he could count on me to do whatever he wished. It was then that he told me the story of the letter from Gilman and of his resolve and practice based on it.

AT THE SUMMIT: JOHNS HOPKINS (1906–1938)

Formerly of great importance and influence, the Department of Zoology at Johns Hopkins had to a considerable degree lost its eminence and was attracting but few graduate students when Jennings arrived on the scene. Brooks, who had earlier turned out a large number of foremost biologists, had grown old and ill and had ceased to be a leader in research. Naturally, he did not represent the currently exciting new lines of work. Jennings had doubtless been brought to Johns Hopkins in the hope that he would reverse the trend. He began by teaching and directing research in areas of experimental zoology, behavior, and general physiology.

Before the first year at Johns Hopkins came to an end, Jennings's own research had shifted to the exciting field of heredity, now revitalized by the rediscovery (1900) of Mendel's papers. He had intended to start work along this line in the summer of 1906, before going to Johns Hopkins, but put it aside to spend the summer in California. After his teaching duties for the first year ended early in 1907, he started what was to prove his major research effort for the next decade: investigation of heredity in Protozoa.

I shall not attempt to recount here the course of Jennings's life at Johns Hopkins in the detail given to his career up to this point. My intention has been to try to expose as fully as the

available evidence permits what went into the making of this man, how he developed into what he became. I do not mean to imply that he did not continue to develop after reaching the summit of his academic success, for he did. He recognized that people come as novices to each stage of their life and that one's experiences continue to modify one throughout life. Nevertheless, by 1906, aged thirty-eight, Jennings's character and capabilities were pretty well determined. What further changes occurred during the next seventeen years can only be guessed, for he either lacked the time or the inclination to keep a diary during this period, and very few of his letters have come to my attention. On the contrary, many large volumes of diaries record his life, work, and thought from 1923 to 1945. These I have only sampled and so am not yet prepared to use to full advantage. For the most part, therefore, the remainder of this biography will be mainly an account of events and accomplishments. In those respects, the years at Johns Hopkins consist chiefly of two widely different periods: one of intensive investigation (1907–1916) and one of varied activities (1917–1937).

Jennings's work on genetics followed the same general pattern as his work on behavior. In both fields, he began by investigating as thoroughly as was then possible a single, relatively simple organism. He then made a comparative study of other organisms at about the same level of complexity, other ciliates and other Protozoa, following this with studies of multicellular organisms. At each step in the sequence of studies, he noted the special features exhibited by each organism and the common features or generalities shown by organisms at similar or different levels of complexity, ending with the fundamentals and their implications for biology and for man. Finally, he synthesized this approach to the two fields of behavior and genetics into a beautiful, integrated view of science, philosophy, and the practice of human living.

During the years at Johns Hopkins, especially during the

first decade when no longer engaged in experimental work on behavior, he carried on lively discussions of the significance of the behavior work in a number of book reviews and general papers. He identified the behavioral properties of cells and organisms with the properties of their supramolecular levels of organization of matter. His radically experimental analyses led him thus to a monistic view in which mind could not be separated as distinct from matter. The human mind and human behavior were as determined in their operation as those of lower organisms, and they operated on the same basic principle of the interaction of outer factors with inner structural factors. In the lower and higher organisms, and in man, behavior was viewed as determined, though at increasing levels of complexity, by the properties of organismic structure and its responses to previous experience. Behavior was shown to be modifiable by experience, the modification having a material basis in altered physiological states. In man, these experiences included perception of outer events and such inner events as sensations, feelings, emotion, and thought, all themselves properties of the highly complex material organization of man. This view, obviously far removed from the views of the simplistic mechanists, likewise left no place for the vitalists' "entelechy" or "élan vital."

Towards the end of this career, Jennings shifted his focus from the level of the cell and the individual organism to the social level of groups. Again he began with paramecia, seeing in their mating behavior the beginnings of the development of social systems and social behavior. He also gave some attention to social behavior and organization in higher organisms and would doubtless have carried this much further had he been able to remain active longer.

His genetics studies, begun in 1907, came at a time when leaders in biological research were attempting to test the generality of Mendel's laws. Initially discovered in work on

higher plants, they were soon extended to higher animals by Bateson in England and by Cuénot in France. This work settled the question of generality for all higher organisms. It left open, however, the questions of how early in evolution these laws began to operate, whether they evolved independently in plants and animals, being somehow connected with multicellularity, and whether some more primitive and simpler mechanism of heredity existed in unicellular organisms. There was also a need to find organisms that would be more favorable for pushing genetic analysis still further. All of these considerations were probably in Jennings's mind when he made the decision to shift from work on behavior to work in the new field of genetics. He probably also foresaw the ultimate desirability of examining the possibility of hereditary individual differences in behavior. For reasons that will become evident, he did not succeed in establishing unicellular organisms as the most favorable material for genetic analysis. T. H. Morgan's work, begun two years after Jennings started work on *Paramecium,* established the fruit fly, *Drosophila,* as the choice organism at that time and for decades to come; but eventually—more than thirty years later—Jennings's decision to turn to the simplest organisms was vindicated by a great period in which others used them for the deepest and most fundamental penetration into genetics. Jennings barely lived to see the beginnings of this movement; he died before it reached its greatest achievements. His choice of paramecia was premature and he did not go far enough in his choice of simple organisms. The bacteria and their viruses proved in the 1940s to be the rewarding materials. Nevertheless, Jennings laid broad and deep foundations for all later work on the genetics of the Protozoa.

In this new field, his earliest studies (1908) were made on the processes of reproduction in paramecia. They showed—contrary to prevalent opinion, including his own—that they were fundamentally the same as in higher, multicellular or-

ganisms. This was an essential step toward the ultimate unification of genetics. He then proceeded to establish, with characteristic abundance of quantitative data, that the asexual progeny of a single cell—a clone—of *Paramecium* exhibited genetic constancy. Variations among the cells of a clone were due to diverse environmental conditions or to stages of growth and development. In other words, they were phenotypic, not genotypic, diversities. The principle of the genetic uniformity and constancy of the clone, established first for *Paramecium* and by his students for other ciliates, was later extended by other students to asexually reproducing multicellular organisms (*Hydra,* rotifers). This has remained a basic principle of genetics for all organisms that form clones.

Jennings then turned (1910–1913) to the study of heredity in the sexual reproduction, conjugation, of *Paramecium.* This was to be the test of whether Mendelian laws, or some simpler or different laws, held for unicellular organisms. But the test required making crosses between the members of genetically different clones. To his great disappointment, he was unable to make the necessary crosses. There was no lack of paramecia differing in visible hereditary characters, but the different types refused to mate with one another. In fact, he found that the conditions required for mating to occur were different for the visibly different clones, so that when two kinds were grown together, each mated only with its own kind, even when both kinds were mating at the same time in the same culture vessel. The explanation of this annoying limitation on analysis and the discovery of the means of circumventing it did not come until a quarter of a century later.

Meanwhile, Jennings proceeded to accomplish what he could within the technical limitations imposed at that time. He showed that conjugation between paramecia of the same kind produced many hereditarily diverse clones. This, of course, agreed in a general way with expectations based on Mendelin

laws, if the initial paramecia were heterozygous, *i.e.,* genetically impure. However, he could not test this directly, because he was unable to make crosses among the diverse clones thus produced.

So, he approached the matter indirectly. If the variations were due to genic recombination, such variations should not arise at conjugation in genetically pure (homozygous) paramecia and homozygosity should be producible by successive inbreedings. In the same way, Johannsen had obtained pure-breeding lines of beans by successive inbreedings. To his astonishment, he continued to obtain hereditary diversities in abundance in spite of successive self-fertilizations. His contemporary, Victor Jollos, obtained comparable results and concluded that the hereditary variations that both he and Jennings observed were not due to Mendelian phenomena, but to temporarily persistent variations (*Dauermodifkationen*) in expression of a constant, pure genotype. Jennings, however, was unwilling to accept this interpretation without exploring the possibility that the variations might be due to an initial very high degree of genetic impurity (heterozygosity) that would still be high after a limited number of successive self-fertilizations.

This led him to calculate the mathematical expectations on Mendelian theory. His calculations made this explanation unlikely and he cautiously concluded that Mendelian shuffling of the genes might not be the whole of the matter. Nevertheless, the erratic nature of Jollos's results prevented him from accepting Jollos's interpretation. Twenty years later, Jennings's students showed that pure-breeding lines of paramecia could in fact be selected and that some of the variability was due to mechanisms other than Mendelian recombination. Only later, very near the end of Jennings's life and too late for him to assimilate it, did the beginnings of a full understanding of the matter emerge from observations of his former student, Sonneborn, on "nuclear differentiation." After his death, discoveries

of the transient and persistent regulations of genetic activity via repression and derepression mechanisms further clarified the situation.

Jennings's excursion into the mathematics of heredity (1911–1924) was a delightful exercise of his talent for mathematics. During some periods of his life, he would start his day with pure mathematical studies for the sheer love of them. His late but joyous encounter with calculus called forth the conviction that its study should come at the beginning of a biologist's training. With such proclivities, his long and varied pursuit of mathematical applications to biological problems was inevitable. The earliest (1911–1917) applications, those directed to the analysis of successive inbreedings in paramecia, led him to pursue the analysis for various systems of breeding in a series of contributions that were among the first in what was to develop, in the hands of Fisher, Wright, Haldane, and their followers, into the important discipline of mathematical or population genetics. Later (1918–1924), Jennings applied these talents to the analysis of the theory of the linear arrangement of the genes in the chromosomes, using the data of the Morgan School on crossing-over and interference in *Drosophila*. In the midst of these studies, he gave one of the evening lectures at the Woods Hole Marine Biological Laboratory on the subject of the theory of the linear arrangement of genes in the chromosome.

I have heard that the events were somewhat as follows. The lecture was announced as a critique of the theory, without any indication of which side of the current controversy Jennings would attack or defend. Morgan and his co-workers were at Woods Hole at the time and Morgan fully appreciated Jennings's mental power and influence. So before the lecture he made it his business to seek out Jennings, give him the latest data, and convey to him the confidence his group had in their interpretations. Perhaps, in his affection for Jennings, Morgan

didn't want him to make a fool of himself, as if that were possible; but in this case, the data were rather abstruse and not widely understood or appreciated. Jennings gave Morgan no clue of what he would say in his lecture.

When the time came, Morgan and his cohort were sitting in the front row prepared to defend themselves from the anticipated attack. Instead of attacking, however, Jennings showed that the complex set of data fully justified the interpretation made and could hardly be reconciled with any theory that was not essentially the same. After the lecture, Morgan rushed to the speaker's platform and threw his arms around Jennings.

Meanwhile, Jennings was struggling with the problem of evolution. He was unwilling to accept as final his demonstration of the genetic constancy of the clone, but sought "evolution in progress." Surprisingly, he sought it in change of heredity within a clone. For this sort of work, involving selections, paramecia were not favorable; it was impossible to select for small hereditary differences in characteristics that were so phenotypically variable during growth and development and so responsive to environmental variables. So he hit upon the much more favorable shelled rhizopod, *Difflugia*. Its shell (or "test") was formed at the time of cell division and then persisted unchanged. Selection for variations in shell characteristics eventually yielded (1916) within a clone minute but statistically significant differences that persisted for some generations in the absence of further selection. This welcome result was held by Jennings to be "evolution in progress." Although this work was important for the thinking of his contemporaries, the basis of the diversities selected and their durability remained obscure and has not to this day been clarified—except for one special case of outstanding significance.

This case, returned to in the 1930s and reported in full in 1937, concerned the so-called mouth and teeth of the shell.

The mouth is merely a circular aperture in the shell and the teeth are a circlet of small projections from the rim of the mouth. During reproduction, half of the cell mass extends through the mouth and is at first naked, a new shell with mouth and teeth forming on it before the cell divides into two. Remarkably, the mouth and teeth of the new shell are formed in juxtaposition to those of the existing shell, each tooth of the new shell forming in the space between two of the teeth of the old shell by what we would now call a "negative template" mechanism. Jennings's experiments included removing some or all of the teeth and some of the adjacent shell, with demonstration of their correlated effects on the shell of the daughter cell. Many years later, in the 1950s (after Jennings had died), the discovery of "template replication" in the reproduction of genic DNA prepared biologists to appreciate the significance of Jennings's discovery of a comparable process at the supramolecular level of structure.

After his basic studies of 1907–1916, which culminated with the conclusion that he had demonstrated evolution in progress, Jennings became interested in the causes and nature of these "evolutionary" variations. In his day, Lamarckism was still defended in some quarters on the basis of purported observations and experiments, especially by Kammerer. Jennings repeatedly reviewed the evidence critically and stimulated students to undertake studies of the possible inheritance of characteristics acquired as a result of environmental action. He was well aware of the alternative of selection of spontaneous or undirected mutations, but he kept an open mind while demanding critical evidence.

I was one of the students he stimulated to undertake such experiments. I recall vividly his questions and comments on this topic during my oral examination for the Ph.D. degree in 1928. After asking me about the work in a number of other laboratories on this topic, he then asked what had become of

the investigators. Fortunately, I knew that most of them had committed suicide or gone out of their minds. He concluded with: "Let that be a lesson to you!"

From 1916 until the early 1930s, Jennings published only one laboratory investigation, but he directed the researches of many students. Some of them (including Stocking and Middleton) carried on studies of *Paramecium* and other ciliates; others (including Root, Hegner, and Taliaferro) extended to other rhizopods the kind of study he had made on *Difflugia;* and some extended work to multicellular organisms. Karl Lashley, later famous as a psychologist, who was probably attracted to Jennings because of his work on behavior, found Jennings steeped in genetics and, entering into the spirit of the laboratory, was the first student to extend the genetic work to multicellular organisms. He did his thesis research (1911–1915) on inheritance of tentacle number in *Hydra.* Soon thereafter (1917–1920) Jennings inspired Bessie Noyes to carry on genetic work with rotifers, the organisms on which he had made his first extensive studies, in the 1890s. Beginning in 1920, he also turned to rotifers, along with his assistant, Ruth Stocking Lynch. The pressure of other duties and commitments prevented him from concentrating on his work. It was done intermittently, largely in summers, and the statistical analyses and writing dragged on for years. Finally, the results appeared in 1928 in two papers on the life cycle of *Proales* during parthenogenetic reproduction and on factors, particularly maternal age, affecting fecundity and length of life. Among other students participating in the program on multicellular organisms were J. Finesinger and Helen Miller (Costello) working on a rotifer, Emily Emmart on rotifers and *Gammarus,* and Sonneborn on the flatworm *Stenostomum.*

Jennings meanwhile was developing his views of the evolutionary process, which he published repeatedly. They were based solidly on the *Drosophila* work of Morgan's laboratory,

especially on the series of multiple alleles and specific modifying factors affecting eye color. These provided ample evidence for the minutest hereditary variations; hence they supplied the materials for the operation of Darwinian natural selection of almost imperceptible gradual changes. The demonstrated genetic complexity of an apparently simple character led Jennings to stress strongly the basic error in the notion that each of the kinds of unit characters under study was determined by only one gene.

In 1930, with support of a grant from the Rockefeller Foundation, Jennings returned for a few years to a reinvestigation of the genetics of paramecia. He soon lost heart in it, however, because of his inability to cross genetically diverse clones, so he went back to *Difflugia.*

At this time, I was his research assistant. I asked, and he generously gave, permission for me to continue to work with *Paramecium* with the objective of putting it in condition for standard Mendelian analysis. His generosity paid off in 1937 with my discovery of mating types that made crossbreeding and Mendelian analysis at least as easy as in higher organisms and that added certain additional advantages for classical genetic analysis. He was overjoyed with this new turn of events and came back himself to a renewed investigation of the genetics of paramecia, choosing the species *P. bursaria,* while I continued to work with *P. aurelia.* At this time, Jennings was sixty-nine, a year from retirement; but he was still able to carry on exhausting and exhaustive laboratory work with remarkable vigor and intellectual power. The story of this work, done mainly after his retirement, will be told presently. First, however, to complete the picture of his thirty-two years at Johns Hopkins, let me try to portray the life he led at Johns Hopkins while the researches and writings mentioned above were in progress.

Jennings's early years (1906–1910) at Johns Hopkins were golden: exceptionally light teaching duties, ample opportunities

for research, no administrative responsibilities. He threw himself with astounding intensity into genetic research and publication, while maintaining interest in behavior through teaching, outside lectures, and publications. His work almost cut him off from the prized luxury of correspondence with family and friends. This was one price he had to pay for what he called the "inhuman" concentrated pursuit of scientific investigation. On the other hand, there were rewards, both in the joy of research and in high recognition. The first of several honorary degrees was conferred in 1909 (by Clark University); he was elected President of the American Society of Zoologists in 1908 and to membership in the National Academy of Sciences at the relatively young age of forty-six (1914).

His elevation to the position of Director of the Zoological Laboratory in 1910 naturally brought about great changes in his life. One of his first moves (1911) was to fill the position left vacant by his own promotion. He brought in S. O. Mast, whose research he had supervised and found impressive during the summer of 1903 at Michigan. Now that Jennings had turned to genetics, Mast took over the work in general physiology. Jennings had driven himself so hard in research that by 1911 it began to tell on his health; he had to curtail greatly his working hours. He tried to recover his strength during the summer of 1911 by a trip to France and England, which he greatly enjoyed, for it satisfied his recurrent longing to expand his horizons beyond the confines of the laboratory to the whole range of the great works of man.

Jennings's level head, keen mind, sound judgment, and objectivity were soon recognized and exploited by his university colleagues. The Academic Council had been appointed by the President prior to 1912; thereafter it was elected by the faculty. At the first election, Jennings was overwhelming first choice; he was elected continuously thereafter until 1934. In the affairs of the university, he was a foremost spokesman for the faculty

and was increasingly called upon to chair or serve on the most important university committees. When the university administration made what he dubbed "half-hearted" attempts to discontinue the undergraduate college and concentrate on graduate work, Jennings led the faculty in an unsuccessful effort to bring this about. As the years wore on and he became increasingly taken up with university affairs, he commented sadly that the decline of scholarly work by professors as they grew older was not due to failing powers or interest but to their being put on committees.

Within his own department, the story was similar. Administrative work absorbed increasing amounts of his time and energy, leaving less and less for laboratory research. For a few years he managed to keep at it pretty vigorously along with a group of students, especially Lashley, Root, Ruth Stocking, and Middleton. Together they presented a symposium on the genetics of lower organisms at the December 1914 meeting of the American Association for the Advancement of Science. The importance and influence of the Johns Hopkins laboratory was again on the rise, fulfilling the design of Brooks. When the School of Hygiene and Public Health was created (1918) at Johns Hopkins, several of Jennings's students, including Hegner and Taliaferro, were chosen to be on its faculty.

After World War I, the number of students in Jennings's department increased to a point that made Jennings deplore the diffusion and dilution of attention to them. He wrote, "I am not good at keeping contact with so many lines of work. Concentration is my successful method." A stream of visitors flowed to the department, and this led Jennings to write: "There is nothing that utterly destroys all chance for scientific investigation or any continuous work, like having a Distinguished Guest on your hands": but, nevertheless, he enjoyed these contacts. He summed up his situation in these words: "There is a strong push toward forcing the head of a department into the position

of a factotum, a servant that attends to all sorts of things to further the work of others, but with no opportunity to do serious work himself." Some relief came in 1919 with the appointment of his former student, Ruth Stocking Lynch, as his assistant in both research and office work, but this hardly offset the increase in demands on him.

Nevertheless, Jennings came to realize that he was much appreciated. In 1921, his students, colleagues, and friends presented him with a volume of appreciative letters and joined together in a celebration of the twenty-fifth anniversary of his doctorate. They had Linton paint his portrait, which was eloquently presented to the university by his distinguished colleague, the philosopher Lovejoy. At a festive dinner, his former Harvard teacher, Davenport, summarized his contributions to science and Jennings responded with one of his most charming essays, "On the Advantages of Growing Old." This recognition was of course well deserved and heartily bestowed. Jennings had thrilled many students with his scholarly and penetrating courses on behavior, development, genetics, and evolution. He had opened their minds to the broader aspects of biology and its philosophical overtones in seminars on the method and nature of science, on the history of biological theories, on the body–mind problem, on vitalism and mechanism, on the implications of physical relativity and indeterminism for biology, on eugenics and the race problem, on the relation of biology to human affairs, and on creative and emergent evolution. For some years these seminars were held in the evenings at his home, until they became too much for his wife and eventually for him also. The combination of uncompromising respect for significant facts down to the minutest detail with the broad scope of his encompassing mind was fully appreciated by his students, who considered working with him a treasured privilege.

And, reciprocally, he appreciated his students, perhaps more

than they deserved. The year (1928) that I received my Ph.D., he and Mrs. Jennings invited all those receiving their degrees to dinner at their home. After dinner, he made a little speech. He told a bit about each of a number of previous Ph.D.s from the department, showing their pictures and telling of their successes after leaving Johns Hopkins. He concluded with the statement that in his opinion those who were now receiving their Ph.D.s were in no way inferior to those he had been speaking of. No wonder his students adored him!

Jennings's eminence naturally led to participation in many off-campus affairs. He held high office and took part in the work of many national and international biological, psychological, and philosophical societies and meetings (see appended list). He served during World War I with the Food Administration in Washington, D.C. He testified before Congress on immigration policy. After serving five years (1920–1925) with the National Research Council, he was happy to terminate that committee work, for he thought he was not suited to it. Widely sought as a speaker on a great variety of topics by many professional and lay groups, he found it difficult not to accept.

He wore down periodically from sustained tenseness and overwork. When in this condition he used to say: "I am H. S. Jennings only a few hours per day." In order to put his physiology back in working order, he not only cut down working hours but turned to other interests, such as music and literature. Most evenings he played chamber music records and read aloud with his wife and son. He even tried to learn to play the clarinet so he could join local chamber music groups, but he never made much of a success of this and regretted that he was too deliberate to be freely rhythmic. His favorite reading was Pepys's *Diary,* biographies, histories (returning periodically to Gibbon), Elizabethan drama, and some novels, like *Gil Blas.* Such recreation, freedom from evening engagements, and going

early to bed restored him so completely that he never felt better—until he was down again, and again became worried and discouraged.

Two events of the mid-1920s particularly lifted his spirits: the Leidy Award of the Philadelphia Academy of Natural Sciences, which prompted him to write, "A bit of recognition of this sort quite cheers one up when he wonders if he isn't dropping behind," and an offer from Stanford University, which he did not accept but which prompted his comment that there was "a certain satisfaction in letting authorities here know that they cannot keep men on the salaries they pay." The President of Johns Hopkins took a different view; he thought it worth so much to be at Johns Hopkins that there was no need to match salary offers from elsewhere.

Nothing gave Jennings more pleasure or sent his spirits soaring higher than opportunities to get away for an extended period from the press of duties at Johns Hopkins. For many years he escaped from the Baltimore heat as soon as possible after the spring semester, spending the summer at the Marine Biological Laboratory in Woods Hole, often with assistants and students, researching and enjoying contacts with the biologists there. Two joyous summers (1925 and 1926) were spent at the Pacific Grove Station of Stanford, where he gave lectures based on those already prepared for courses at Johns Hopkins, so that he was relatively free. And he spent two of the happiest and most wonderful years of his life as Visiting Professor at Keio University, Tokyo, in 1931–1932, and as George Eastman Visiting Professor at Oxford (1935–1936). His diaries tell the day-to-day tale of these richly varied experiences he shared with his wife.

In one very important respect the increasing complexity of Jennings's life had a most valuable effect. Unable to find the long continuous periods needed for laboratory research, he

could in shorter periods prepare and give outside lectures or write and publish essays and books about the matters he dealt with at length in his courses and seminars. Using his gifts for clear thinking and for abstracting main ideas, together with his extraordinary talent for exposition in lucid, engaging language, he became an eminently successful educator of biologists, people in related fields, and the reading public. In the early decades of genetic studies, he was a leader in publicizing its main concepts and their significance for man. He expounded the import of genetics and general biology for the philosopher, the sociologist, the psychologist, the psychiatrist, public health workers, and the ordinary layman. He preached caution and sense to the eugenicists, recognizing the desirability but slowness of feasible eugenic action and the speed with which man's urgent, immediate needs could be met by improving his conditions of life. He saw no threat of genetic deterioration from medical cures or public health measures, which to him were but a continuation of man's evolved gift of the power to overcome his deficiencies.

He published many articles on these and other themes and gathered his ideas together in the popular book, *The Biological Basis of Human Nature* (1930). The ground had been prepared by his little booklet, *Prometheus or Biology and the Advancement of Man* (1925). His textbook, *Genetics* (1935), was focused on principles; it was not rich enough in detail to comply with the notions of college professors as to what a textbook should be. As one reads through these three books some forty years after their publication, one is surprised and impressed to find how little they would have to be changed to conform to the present state of knowledge and understanding. Of course, much more has been discovered, and genetics has been molecularized; but Jennings recognized, from what was then known, what would be the enduring main principles and their significance for biology and man. Stands taken later by his most knowledgeable and

imaginative successors are clearly and prophetically set forth in those three books.

In my opinion, however, the greatest and perhaps the most enduring of Jennings's books is *The Universe and Life* (1933). This small book, originally presented as three Terry Lectures at Yale, sets forth beautifully his view of the world and man's place in it. It synthesizes harmoniously what his studies of behavior and genetics had taught him. Each human being is initially unique in his genetic endowment and develops uniquely. The exception to genetic uniqueness—identical twins—is no exception to uniqueness of development. To that there is absolutely no exception. The brain, with all its complexity of structure and capacity for functioning, is genetically determined to develop. Development, of course, includes alterations in mental structure as a result of experiences, and each such change in the material structure of the mind affects its later responses in the form of behavior and of further material change of mental structure. Each step in this continual interplay between experience and the mind is completely determined, in the sense that the effect of each experience is determined by the current state of the brain, itself a resultant of the effects of the whole sequence of previous experiences on the brain–mind structure and functioning. The development of mind in each individual, although determined at each step, is nevertheless unique and unpredictable, because, if for no other reason, of the individual's unique and unpredictable sequence of experiences. In the sense of being free from the step-by-step determinisms operating in any other individual, each individual is free and capable of making choices unique to himself. If each individual is free, unpredictable, and unique (though determined), then so is each generation of man. (If this is not demonstrated by the average man, it surely is by the great men, who put their stamp on their times.) In this Jennings saw man's greatest hope:

What has failed in the past need not fail in the future. The unpredictable future of man will be what man chooses to make it, and that no one can foresee.

THE FINAL YEARS (1937–1947)

Jennings was sixty-nine, a year shy of mandatory retirement, when he began the series of investigations on the genetics of *Paramecium bursaria.* A gay seventieth birthday party was given for him by his students—gay because it was not an end but a beginning. He would now be free for the concentrated research that he had foregone for so many years. The research he wanted to do looked promising, and he was still strong and active enough to make the most of his freedom. So, in 1938 he became Emeritus Professor and a full time researcher.

Before long his happiness was darkened by his wife's illness. She died in November, 1938. His diaries tell touchingly of his sadness at the loss of the woman with whom he had forty years of beautiful married life. His son and daughter-in-law, Francina Snyder Jennings, lived with him. She was devoted to him and did much to help him through this difficult period.

Fortunately, he was already committed to organize a symposium on the new mating type work for the Christmas meeting of the AAAS at Richmond, Virginia. He threw his energies into this task. He had to give a large part of the symposium himself, not only the general introduction and his own paper on *P. bursaria,* but also Sonneborn's paper on *P. aurelia,* for Sonneborn fell ill with measles just a few days before the meeting. At the symposium, Jennings was a tremendous success. He projected live through the microscope onto a big screen the spectacular agglutinative mating reaction that occurs immediately when cultures of *Paramecium* of complementary mating type are brought together. More than thirty years earlier he had used the same method in Chicago to demonstrate how paramecia aggregate in a region of weak acid.

Immediately after the Richmond meeting, Jennings packed up nearly 2000 of his experimental cultures and set off with his assistant, Elizabeth Kirkwood, for Los Angeles, where he was to be Visiting Professor at UCLA for the spring semester. Unable to get a train compartment from Chicago on, he took an upper berth for himself and a lower for his satchels of culture vials, which he nursed along with tender care. In spite of this, most of the cultures were dead on arrival. But duplicates mailed from Baltimore arrived safely, and Jennings was soon set up to continue his researches while giving a much appreciated course and seminar on genetics of the protozoa. Again teaching proved a severe strain, and he rejoiced when his last class ended, to hearty applause, in May 1939. During the following summer, arrangements were made for him to stay on as Research Associate at UCLA. With support for research assistance obtained from the Carnegie Corporation and from the Committee on Sex Research of the National Research Council, he was able to engage T. T. Chen as cytologist. Chen had worked with him at Johns Hopkins. He also engaged a number of junior assistants, including especially Elizabeth Hegglund, and eventually Ruth Stocking Lynch, who had long been his associate at Johns Hopkins.

His diary of the first year at UCLA records day after day his fearful loneliness, in spite of the presence of co-workers, friends and relatives. His niece, Carolyn Jennings, who taught biology at Los Angeles City College, had long been a great admirer of her uncle; she brought him days of joy at parties and on expeditions. Her mother, Lulu, the widow of his only brother, frequently had him for meals. She always had fascinated him, from the time he first saw her when he was a youth in Tonica, Illinois. His interest in Lulu had been kept alive over the years at family gatherings in California and during her visit when the Jenningses were at Oxford. His visits to her home excited him immensely. She was still beautiful. Judging by oblique

entries in his diary, the thought of marriage probably came into both their minds soon after his arrival in Los Angeles. On October 21, 1939, they were married and the fearful loneliness came to an end.

Jennings was still much in demand as a lecturer and continued to comply with invitations through 1943. In 1939, he took part in a symposium at Stanford; he returned during Stanford's Fiftieth Anniversary Celebration in 1941 to give a major lecture, receive an honorary degree, and be made an Honorary Fellow of Stanford University. In 1940, he attended the Bicentennial Celebration of the University of Pennsylvania, again giving a major lecture (the Leidy Lecture) and receiving an honorary degree. In 1941, he gave lectures to a number of California biological societies. For six weeks in 1943, he gave the public Patten Lectures at Indiana University on "Life, Age and Death in Single-celled Organisms in Relation to General Theories of Life and Death." These, I believe, were his last lectures. In the same year came his last honors, an honorary degree from the University of California and election as Honorary Fellow of the Royal Society of Edinburgh.

Then he began to cut down his outside activities, resigning from the Council of the National Academy of Sciences in 1940, after many years of service, and from all other committee work. He confined his work life to research and publication. By 1945 he had brought to publication his whole series of investigation on *P. bursaria* and failed only to finish the book he was writing about them and their general significance, as he had summarized this in his Patten Lectures. The unfinished manuscript of the book based on these lectures is in the Library of the American Philosophical Society.

These last researches, carried on between his sixty-ninth and seventy-fifth years, were unsurpassed in lasting value by any other major investigation of his life, except for his first experimental researches on cell behavior, which had been carried on

between his twenty-eighth and thirty-eighth years. He discovered the existence of systems composed of more than two interbreeding mating types, thus rendering unlikely the possibility that ciliate mating types were early stages in the evolution of male and female. He discovered that *P. bursaria* consists of reproductively isolated subdivisions (varieties, syngens, or biological species) at about the same time Sonneborn was finding this true of *P. aurelia.* In the quarter century since this discovery, all well-studied ciliates and many other unicellular organisms as well have been found to conform to the same principle—the species of the taxonomist is a group of biological species.

Concentrating most of his attention on one of these biological species of *P. bursaria,* Jennings attempted to work out the genetics of its four mating types. Most of his data fit the fairly simple hypothesis of determination by two pairs of unlinked genes, but he had some data that did not fit and therefore remained cautious. Many years after Jennings died, Siegel and collaborators verified the hypothesis and explained most of the exceptions. Others have carried on the genetic work on *P. bursaria* in other exciting directions, all solidly based on Jennings's pioneer work.

Finally, Jennings showed that clones of *P. bursaria* have a life cycle; most of them, at least, pass through periods of immaturity (inability to mate), adolescence, maturity (ability to mate), and senescence, ending in death. The whole cycle lasted several years in some clones under the cultural conditions employed by Jennings, and some did not die by the time he was forced by ill health to stop laboratory work. There was great variability in the length of life and vigor of different clones, some dying immediately after their origin. Two major causes of this variation were identified—one was the age of the parent clones; the other was the relationship between the parent clones. Inbreeding and old parents yielded few or no vigorous daughter

clones; outbreeding and young parents yielded the highest proportions of vigorous long-lived daughter clones. The decisive factors were thus both genetic and physiological. Jennings concluded that natural death did not arise first, as some held, with the evolution of multicellular organisms; but he did not exclude the possibility that some clones might be immortal; some did not die during several years of culture. This study of aging and death was too heroic a task for even younger men to follow up in so long-lived a species; but other investigators, following the same general plan with more favorable species of *Paramecium,* succeeded in confirming the essential features of the life cycle and showed that in these species all clones eventually die, only sexual progeny surviving by initiating new life cycles.

The demonstration by Jennings of the existence of a clonal life cycle and of the role of conjugation in initiating new cycles ran counter to opinions he had previously maintained. Thirty years earlier, under the influence of the then new genetics and of his own overwhelming evidence for the production at conjugation of hereditary variations, including variations in vigor, he interpreted "rejuvenescence" after conjugation as merely one class of the genetic variations. He was also unwilling to exclude the possibility, to a certain degree supported by available evidence, that the apparent aging and death of clones was a reflection of the cumulative effect of unfavorable cultural conditions. Only after he had himself exhaustively investigated the matter during his last years of research activity did he change his views and bring all of the facts into a coherent interpretation. This was typical of the man. In his earliest behavior work he had declared that he didn't care how the experiments turned out, he wanted only to discover the facts and their meaning. And so it was until his last work. It mattered not what he had published thirty years before; all that mattered were the facts and their meaning.

Jennings was genuinely amazed throughout his life at his own success. He bore his eminence and honors modestly. Always high-strung, jerky, energetic, he threw himself completely into every task he undertook, whether it was to his liking or not. He was a man immensely capable both of concentration and of enjoyment. Although a keen observer of people, including himself and his ills, he took people as he found them. He shared his physician–father's skepticism about drugs and medical care; during most of his life he largely ministered to himself on the basis of observations and experiments on himself. He even used glasses bought at the five-and-ten-cent store, for he apparently needed only magnification and that only for fine print. He was decidedly an intellectual, quick but deliberate of mind. His class and public lectures never called attention to himself as a person. With no trace of theatricality, he depended on fully or largely written out, clear, logical, vivid formulations of what he wanted to say. On the whole, his incalculable influence on those who made contact with him was achieved mainly by the example he set of freedom from pettiness, recognition of and concentration on fundamentals, profound respect for both objective investigation and the search for meaning, and an exquisite just balance in dealing with fact and thought.

Only during his last year or two did his health fail to the point at which serious productive work became impossible for even his extraordinary drive. During the last two months he gradually sank while in the Santa Monica Hospital; he died April 14, 1947, a week after his seventy-ninth birthday.

HONORS AND DISTINCTIONS

ACADEMIC CAREER

1888–1889	Assistant Professor of Botany, Texas State Agricultural and Mechanical College
1892–1894	Assistant in Zoology, University of Michigan
1893	B.S., University of Michigan
1894–1895	Assistant in Zoology, Harvard University
1895	M.A., Harvard University
1895–1896	Morgan Fellow, Harvard University
1896	Ph.D., Harvard University
1896–1897	Parker Travelling Fellow (Harvard University), Jena, Germany, and Naples, Italy
1897–1898	Professor of Botany and Bacteriology, Montana State Agricultural and Mechanical College
1898–1899	Instructor in Zoology, Dartmouth College
1899–1901	Instructor in Zoology, University of Michigan
1901	Acting Director, U.S. Fish Commission, Biological Survey of the Great Lakes
1901–1903	Assistant Professor of Zoology, University of Michigan
1902	Director, U.S. Fish Commission, Biological Survey of the Great Lakes
1903–1904	Research Assistant, Carnegie Institution of Washington, Naples Zoological Station
1903–1906	Assistant Professor of Zoology, University of Pennsylvania
1906–1907	Associate Professor of Physiological Zoology, Johns Hopkins University
1907–1910	Professor of Experimental Zoology, Johns Hopkins University
1910–1938	Henry Walters Professor and Director of the Zoological Laboratory, Johns Hopkins University
1938–1947	Emeritus Professor, Johns Hopkins University
1939–1947	Research Associate, University of California

HONORARY DEGREES

1909	Ll.D., Clark University
1918	Sc.D., University of Michigan
1933	Sc.D., University of Pennsylvania

1933	Ll.D., Oberlin College
1935	A.M., Oxford University
1940	Ll.D., University of Pennsylvania
1941	Ll.D., University of Chicago
1943	Ll.D., University of California

VISITING LECTURESHIPS AND PROFESSORSHIPS

1925	Stanford University
1931	Keio University, Tokyo, Japan
1933	Terry Lecturer, Yale University
1934	Vanuxem Lecturer, Princeton University
1935–1936	Eastman Visiting Professor, Oxford University
1939	University of California at Los Angeles
1940	Leidy Lecturer, University of Pennsylvania
1943	Patten Lecturer, Indiana University

AWARDS

1896 and 1908	Walker Prize, Boston Society of Natural History
1925	Leidy Award, Philadelphia Academy of Natural Sciences
1931	One of 14 scientists to have name inscribed in Buhl Hall of Science, Pennsylvania State College for Women

MEMBERSHIPS

1918–1924 and 1928–1936	Member of the Council of the American Philosophical Society
1920–1925	National Research Council, Division of Biology and Agriculture
1928–1931	Chairman of the Bache Fund, National Academy of Sciences
1934–1940	Member of the Council, National Academy of Sciences

CORRESPONDING MEMBERSHIPS

Academy of Natural Sciences, Philadelphia
Russian Academy of Sciences
Société de Biologie de France

HONORARY FELLOW

Royal Microscopical Society, London
Royal Society, Edinburgh

EDITORIAL BOARDS

Biological Bulletin, Genetics, Human Biology, Journal of Experimental Zoology, Journal of Comparative Psychology

PROFESSIONAL SOCIETIES AND OFFICES

American Society of Zoologists (President, 1909)
American Society of Naturalists (President, 1910)
Fellow of the American Association for the Advancement of Science (Vice-President, Section F, Zoology, 1925, and member of Committee of 100 on Scientific Research)
Genetics Society of America (First Chairman, 1922)
Society of Experimental Biology and Medicine
Eugenics Research Association

MISCELLANEOUS

1905–1938	Trustee, Marine Biological Laboratory, Woods Hole, Massachusetts (Trustee emeritus, 1938–1947)
1912–1933	Academic Council, Johns Hopkins University (except for years away from Baltimore)
1917–1918	Statistician, Sugar Division of U.S. Food Administration
1932–1940	Educational Advisory Board of the Guggenheim Foundation

SOURCE MATERIALS

The Jennings collection in the Library of the American Philosophical Society contains all of the source material: diaries, autobiographical sketch, correspondence, commonplace books, and many other documents, including his father's autobiography.

Biographies, Obituaries, and other Published Articles on Jennings

Conklin, E. G., 1947. Herbert Spencer Jennings. In: *Biographical Memoirs of the American Philosophical Society,* pp. 258–62. Philadelphia: The Society.

Carnegie Foundation for Advancement of Teaching, 42d Report, 1946–47, pp. 78–79.

Davenport, C., 1922. Jennings' research. Johns Hopkins Alumni Mag., 10(2):87–92.

Dobell, C., 1947. Herbert Spencer Jennings. Nature, 159:834.

Geiser, S. W., 1934. H. S. Jennings, apostle of the scientific spirit. Bioscience, 5(1):3–18.

Jennings, H. S., 1922. On the advantages of growing old. Johns Hopkins Alumni Mag., 10(4):241–51.

Jensen, D. D., 1962. Preface to reprint of *The Behavior of Lower Organisms.* Bloomington: Indiana University Press.

Lovejoy, A. O., 1922. Presentation of the Linton portrait of Jennings to the Johns Hopkins University. Johns Hopkins Alumni Mag., 10(2):81–86. (An account of Jennings's scientific character.)

Schneirla, T. C., 1947. Herbert Spencer Jennings. Am. J. Psychol., 60:447–50.

Sonneborn, T. M., 1947. Herbert Spencer Jennings. Johns Hopkins Alumni Mag., 35(4):135–38.

Sonneborn, T. M., 1948. Herbert Spencer Jennings. Anat. Rec., 100(2):401–3.

Sonneborn, T. M., 1948. Herbert Spencer Jennings. Genetics, 33: 1–4.

Sonneborn, T. M., 1973. Herbert Spencer Jennings. In: *Dictionary of American Biography.* New York: Charles Scribner's Sons.

BIBLIOGRAPHY

KEY TO ABBREVIATIONS

Am. Nat. = American Naturalist
Am. J. Physiol. = American Journal of Physiology
Am. J. Psychol. = American Journal of Psychology
Anat. Rec. = Anatomical Record
Biol. Bull. = Biological Bulletin
Biol. Symp. = Biological Symposia
Bull. Mich. Fish Comm. = Bulletin of the Michigan Fish Commission
J. Comp. Neurol. Psychol. = Journal of Comparative Neurology and Psychology
Johns Hopkins Univ. Circ. = Johns Hopkins University Circular
Johns Hopkins Alumni Mag. = Johns Hopkins Alumni Magazine
J. Exp. Zool. = Journal of Experimental Zoology
J. Philos. Psychol. Sci. Methods = Journal of Philosophy, Psychology and Scientific Methods
Proc. Am. Philos. Soc. = Proceedings of the American Philosophical Society
Proc. ——— Int. Congr. Eugen. = Proceedings of the ——— International Congress of Eugenics
Proc. ——— Int. Congr. Genet. = Proceedings of the ——— International Congress of Genetics
Proc. Natl. Acad. Sci. = Procedings of the National Academy of Sciences of the United States of America
Psychol. Bull. = Psychological Bulletin
Sci. Mon. = Scientific Monthly
Surv. Graphic = Survey Graphic
U.S. Fish Comm. Bull. = United States Fish Commission Bulletin

1890

Some parasitic Fungi of Texas. Texas Agricultural Experiment Station. Bulletin no. 9.

1894

A list of the Rotatoria of the Great Lakes and of some of the inland lakes of Michigan. Bull. Mich. Fish Comm. no. 3, pp. 1–34.

1896

A biological examination of Lake Michigan in the Traverse Bay region. III. Report on the Rotatoria. Bull. Mich. Fish Comm. no. 6, pp. 85–93.

The early development of *Asplanchna Herrickii,* de Guerne. A contribution to developmental mechanics. Bulletin of the Museum of Comparative Zoology, Harvard College, 30(1):1–117.

1897

Studies on reactions to stimuli in unicellular organisms. I. Reactions to chemical, osmotic and mechanical stimuli in the ciliate Infusoria. Journal of Physiology, 21(4 and 5):258–322.

1898

Trochosphaera again. Science, 8(199):551.

1899

Studies on reactions to stimuli in unicellular organisms. II. The mechanism of the motor reactions of Paramecium. Am. J. Physiol., 2(4):311–41.

Studies on reactions to stimuli in unicellular organisms. III. Reactions to localized stimuli in Spirostomum and Stentor. Am. Nat., 33(389):373–89.

Studies on reactions to stimuli in unicellular organisms. IV. Laws of chemotaxis in Paramecium. Am. J. Physiol., 2(4):355–79.

The psychology of a Protozoan. Am. J. Psychol., 10(4):503–15.

1900

The behavior of unicellular organisms. Biology Lectures from the Marine Biology Laboratory of Woods Hole, 1899, pp. 93–112.

Minutes of the Zoological Club of the University of Michigan. Science, 12:886–87.

Minutes of the Zoological Club of the Universtiy of Michigan. Science, 12:927–28.

Studies on reactions to stimuli in unicellular organisms. V. On the movements and motor reflexes of the Flagellata and Ciliata. Am. J. Physiol., 3(6):229–60.

Studies on reactions to stimuli in unicellular organisms. VI. On the reactions of Chilomonas to organic acids. Am. J. Physiol., 3: 397–403.

Rotatoria of the United States, with special reference to those of the Great Lakes. U.S. Fish Comm. Bull. for 1899, pp. 67–104.

A report of work on the Protozoa of Lake Erie, with special reference to the laws of their movements. U.S. Fish Comm. Bull. for 1899, pp. 105–14.

Reactions of Infusoria to chemicals: a criticism. Am. Nat., 34(399): 259–65.

1901

With J. Reighard. *The Anatomy of the Cat.* New York: Henry Holt & Co. 486 pp. Supplemented by *Dissection of the Cat,* by J. Reighard, J. Rush Elliott, and H. S. Jennings. 99 pp.

With F. H. Crosby. Studies on reactions to stimuli in unicellular organisms. VII. The manner in which bacteria react to stimuli, especially to chemical stimuli. Am. J. Physiol., 4:31–37.

On the significance of spiral swimming of organisms. Am. Nat., 35: 369–78.

The Rotatoria. Synopses of North American Invertebrates, no. 17. Am. Nat., 35:725–77.

1902

Artificial imitations of protoplasmic activities, and methods of demonstrating them. Journal of Applied Microscopy and Laboratory Methods, 5(1):1597–1602.

With E. M. Moore. Studies on reactions to stimuli in unicellular organisms. VIII. On the reactions of Infusoria to carbonic and other acids, with special reference to the causes of the gatherings spontaneously formed. Am. J. Physiol., 6(5):233–50.

Studies on reactions to stimuli in unicellular organisms. IX. On the behavior of fixed Infusoria (Stentor and Vorticella), with special reference to the modifiability of Protozoan reactions. Am. J. Physiol., 8:23–60.

With Clara Jamieson. Studies on reactions to stimuli in unicellular organisms. X. The movements and reactions of pieces of ciliate Infusoria. Biol. Bull., 3(5):225–34.

1903

Asymmetry in certain lower organisms and its biological significance. In: *Mark Anniversary Volume,* ed. by G. H. Parker, pp. 317–37. New York: Henry Holt and Co.

Rotatoria of the United States. II. A monograph of the Rattulidae. U.S. Fish Comm. Bull. for 1902, pp. 273–352.

1904

A method demonstrating the external discharge of the contractile vacuole. Zoologischer Anzeiger, 27(1):656–58.

Physical imitations of the activities of Amoeba. Am. Nat., 38(453): 625–42.

The behavior of Paramecium. Additional features and general relations. J. Comp. Neurol. Psychol., 14(6):441–510.

Contributions to the study of the behavior of lower organisms. Carnegie Institution of Washington Publication no. 16.

1905

Editorial. Concerning the genetic relations of types of action. J. Comp. Neurol. Psychol., 15(2):132–37.

The movements and reactions of Amoeba. Biologisches Zentralblatt, 25:92–95.

The basis for taxis and certain other terms in the behavior of Infusoria. J. Comp. Neurol. Psychol., 15(2):138–43.

Papers on reactions to electricity in unicellular organisms. J. Comp. Neurol. Psychol., 15(6):528–34.

Modifiability in behavior. I. Behavior of sea anemone. J. Exp. Zool., 2(4):447–72.

The method of regulation in behavior and in other fields. J. Exp. Zool., 2(4):473–93.

1906

Modifiability in behavior. II. Factors determining direction and character of movement in the earthworm. J. Exp. Zool., 3(3): 435–55.

Behavior of the Lower Organisms. Columbia University Biological Series, no. 10. New York: Macmillan Publishing Co., Inc. xiv + 366 pp. Reprinted, Columbia Univ. Press, 1923; Indiana Univ. Press (Preface by Donald Jensen), 1963. Translated into German by E. Mangold, 1910, Berlin; Tambried, Leipzig, 578 pp.

1907

Behavior of the starfish *Asterias Forreri,* de Loriol. University of California Publications in Zoology, 4(2):53–185.

Formation of habits in the starfish. Johns Hopkins Univ. Circ., new series, no. 3, whole number 195, pp. 16–18.

Review. *Organische Zweckmässigkeit, Entwicklung und Vererbung von Standpunkt der Physiologie,* by Paul Jensen. Science, 25: 665–66.

1908

Animal behavior. Recent work on the behavior of higher animals. Am. Nat., 42:207–16, 355–60.

Animal behavior. Mind in animals. Am. Nat., 42:754–60.

Heredity, variation and evolution in Protozoa. I. The fate of new structural characters in Paramecium, in connection with the problem of the inheritance of acquired characters in unicellular organisms. J. Exp. Zool., 5(4):577–632.

Heredity, variation and evolution in Protozoa. II. Heredity and variation of size and form in Paramecium with studies of growth, environmental action, and selection. Proc. Am. Philos. Soc., 47(190):393–546.

The interpretation of the behavior of lower organisms. Science, 27(696):698–710.

Progress in the study of the behavior of the lower organisms during the past year. Psychol. Bull., 5(6):179–90.

1909

Heredity and variation in the simplest organisms. Am. Nat., 43: 321–37.

The work of J. von Uexküll on the physiology of movements and behavior. J. Comp. Neurol. Psychol., 19:313–36.

Review. *The Birth of Intelligence,* by Georges Bohn. Am. Nat., 43: 619–33.

Review. *The Problem of Age, Growth and Death,* by Charles S. Minot; also *Heredity,* by J. Arthur Thompson. Psychol. Bull., 6(4):140–43.

1910

With George T. Hargitt. Characteristics of the diverse races of Paramecium. J. Morphol., 21(4):495–561.

Diverse ideals and divergent conclusions in the study of behavior in lower organisms. Am. J. Psychol., 21(3):349–70.

Experimental evidence on the effectiveness of selection. Am. Nat., 44:136–45.

The tropisms. Comptes rendus du VIème Congrès international de Psychologie, Genève, 1909, pp. 307–24.

What conditions induce conjugation in Paramecium? J. Exp. Zool., 9:279–300.

1911

Assortative mating, variability and inheritance of size, in the conjugation of Paramecium. J. Exp. Zool., 11(1):1–134.

Pure lines in the study of genetics in lower organisms. Am. Nat., 45:79–89.

Computing correlation in cases where symmetrical tables are commonly used. Am. Nat., 45:123–28.

Computation of the coefficient of correlation. Am. Nat., 45:413.

"Genotype" and "pure line." Science, 34:841–42.

Heredity and personality. Science, 34:902–10.

Vitalism and experimental investigation. Science, 33:927–32.

1912

Age, death and conjugation in the light of work on lower organisms. Popular Science Monthly, 80:563–77.

Driesch's vitalism and experimental indeterminism. Science, 36: 434–35.

Nuclear growth during early development. Am. Nat., 46:366–68.

Production of pure homozygotic organisms from heterozygotes by self-fertilization. Am. Nat., 46:487–91.

1913

The effect of conjugation in Paramecium. J. Exp. Zool., 14:279–391.

With K. S. Lashley. Biparental inheritance and the question of sexuality in Paramecium. J. Exp. Zool., 14:393–466.

With K. S. Lashley. Biparental inheritance of size in Paramecium. J. Exp. Zool., 15:193–99.

Causes and determiners in radically experimental analysis. Am. Nat., 47:349–60.

Doctrines held as vitalism. Am. Nat., 47:385–417.

1914

Life and matter from the standpoint of radically experimental analysis. Johns Hopkins Univ. Circ., new series, 10(270):1162–80.

Development and inheritance in relation to the constitution of the germ. Johns Hopkins Univ. Circ., new series, 10(270):1181–1232.

Formulae for the results of inbreeding. Am. Nat., 48:693–96.

Review. *Moderne Wissenschaft und die Illusionen Professor Bergsons,* by Hugh S. R. Elliot, mit einer Vorrede von E. Ray.

Archiv für Hydrobiologie und Planktonkunde, 9:648–55; also in J. Philos. Psychol. Sci. Methods, 10:353–58.

Tables for computing the results of the distribution of chromosomes and inheritance of Mendelian factors, in biparental reproduction. Johns Hopkins Univ. Circ., new series, 10(270):1233–37.

1916

The numerical results of diverse systems of breeding. Genetics, 1:53–89.

Heredity, variation and the results of selection in the uniparental reproduction of *Difflugia corona*. Genetics, 1:407–534.

The numerical results of diverse systems of breeding. Proc. Natl. Acad. Sci., 2:45–50.

The work of the Department of Zoology. Johns Hopkins Alumni Mag., 4(4):294–303.

1917

Modifying factors and multiple allelomorphs in relation to the results of selection. Am. Nat., 51:301–6.

The numerical results of diverse systems of breeding, with respect to two pairs of characters, linked or independent, with special relation to the effects of linkage. Genetics, 2:97–154.

Observed changes in hereditary characters in relation to evolution. Journal of the Washington Academy of Sciences, 7(10):281–301.

1918

The biology of children in relation to education. In: *Suggestions of Modern Science Concerning Education,* pp. 1–50. New York: Macmillan Publishing Co., Inc. Republished in 1946 by the National Committee for Mental Hygiene.

Disproof of a certain type of theories of crossing-over between chromosomes. Am. Nat., 52:247–61.

The wheel animalcules (Rotatoria). In: *Fresh Water Biology,* by H. B. Ward and G. C. Whipple, pp. 553–620. New York: John Wiley & Sons, Inc.

Mechanism and vitalism. Philos. Rev., 27:577–96.

1919

Organic evolution. In: *American Year Book for 1918,* pp. 672–81. New York: Daniel Appleton & Co.

Experimental determinism and human conduct. J. Philos. Psychol. Sci. Methods, 16:180–83.

1920

Organic evolution. In: *American Year Book for 1919,* pp. 666–70. New York: Daniel Appleton & Co.

Life and Death; Heredity and Evolution in Unicellular Organisms. Boston: Richard G. Badger, Gorham Press, 233 pp. Translated into French by M. Francois-Perey. Felix Alcan, Publ. 267 pp. (1927)

1921

Review. *The Unity of the Organism, or the Organismal Conception of Life,* by W. E. Ritter. Philosophical Review, 30:616–24.

1922

On the advantages of growing old. Johns Hopkins Alumni Mag., 10(4):241–51.

Variation in uniparental reproduction. Am. Nat., 56:5–15.

1923

Crossing-over and the theory that the genes are arranged in the chromosomes in serial order. Proc. Natl. Acad. Sci., 9:141–47.

Inheritance in unicellular organisms. Proc. 2d Int. Congr. Eugenics. Eugenics, Genetics and the Family, 1:59–64.

The numerical relations in the crossing-over of the genes, with a critical examination of the theory that the genes are arranged in a linear series. Genetics, 8:393–457.

The consequences of different degrees of interference in the crossing-over of the hereditary genes. Anat. Rec., 24:404. (A)

Some consequences of different extents of interference in the crossing-over of the genes. Proc. Natl. Acad. Sci., 9:147–49.

Undesirable aliens. Survey, 51:309–12, 364.

1924

Heredity and environment. Sci. Mon., 19:225–38.

An illuminating method of handling data. Science, 59:39.

Proportions of defectives from the northwest and from the southeast of Europe. Science, 59:256–57.

The relative numbers of European-born defectives from the chief

sources of European immigration and the effect of a change in the basis of admission from the census of 1910 to that of 1890. Hearing before the Committee on Immigration and Naturalization, House of Representatives, 68th Congress, first session, Jan. 1924, pp. 512–18.

Acquired characters; reply to Redfield. Science, 59:278.

1925

Review. *Inheritance of Effects of Environmental Conditions,* by Paul Kammerer. Survey, 53:607–8.

Introduction to Seba Eldridge's *The Organization of Life.* New York: T. Y. Crowell Company. 470 pp.

Prometheus or Biology and the Advancement of Man. New York: E. P. Dutton & Co., Inc. vii + 86 pp. Also published, along with others in this series, by Kegan, Paul, Trench, Traubner and Co., London (1933). Translated into Spanish (1926) in Revista de Occidente, 4:75–118. Translated into Chinese (1929).

1926

Organic evolution. In: *American Year Book for 1925,* pp. 915–18. New York: Macmillan Publishing Co., Inc.

Biology and experimentation. Science, 64:97–105.

The inheritance of acquired characters. Forum, 36:702–11.

1927

The biological basis of the family. Surv. Graphic, 12:272–76. Also published in *Family Life Today,* ed. by Margaret E. Rich. Boston: Houghton Mifflin & Co. (1928); Proceedings of the 5th Annual Maryland State Conference of Social Workers; and in Children's Magazine (December).

Diverse doctrines of evolution, their relation to the practice of science and life. Science, 65(1672):19–25. Reprinted with corrections, as *Some Implications of Emergent Evolution.* Hanover, N.H.: Sociological Press. 12 pp.

Organic evolution. In: *American Year Book for 1926,* pp. 902–4. New York: Macmillan Publishing Co., Inc.

Review. *Social Life in the Animal World,* by F. Alverdes. *New York Herald Tribune,* vol. 4, p. 26, Nov. 7.

Review. *Animal Mind,* by Francis Pitt. *New York Herald Tribune,* vol. 4, p. 26, Nov. 7.

Review. *Bipolar Theory of Living Processes,* by G. W. Crile. Nation, pp. 374–77, Oct. 13.

Public health progress and race progress—are they incompatible? Transactions of the 23d Annual Meeting of the National Tuberculosis Association, pp. 1–11. Also published in Science, 66: 45–50, and Journal of Heredity, 18:271–76.

1928

Can we see evolution occurring? In: *Creation by Evolution,* ed. by Frances Mason, pp. 24–33. New York: Macmillan Publishing Co., Inc.

Marriage—a trial? a failure? a conquest? McCall's Magazine, 55:18, 86, 89.

With Ruth Stocking Lynch. Age, mortality, fertility, and individual diversities in the rotifer *Proales sordida,* Gosse. I. Effect of age of the parent on characteristics of the offspring. J. Exp. Zool., 50:345–407.

With Ruth Stocking Lynch. Age, mortality, fertility, and individual diversities in the rotifer *Proales sordida, Gosse.* II. Life-history in relation to mortality and fecundity. J. Exp. Zool., 51:339–81.

What can we hope from eugenics? Plain Talk, 2:399–407.

1929

Genetics of the Protozoa. Bibliographia Genetica, 5:105–330.

1930

Biological aspects of charity. In: *Intelligent Philanthropy,* ed. by E. Faris et al., pp. 270–98. Chicago: Univ. of Chicago Press.

The Biological Basis of Human Nature. New York: W. W. Norton & Co., Inc. xviii + 384 pp. Translated into Spanish, Russian, and Italian.

Heredity and mutation in relation to environment. Collecting Net, 5:81–87.

1931

The cell in relation to its environment. Journal of the Maryland Academy of Sciences, 11(1):25–32.

How heredity affects personality. Parent's Magazine, 6(4):17, 65–67.

Nature and nurture. Surv. Graphic, 19(1):7–11, 70–71.

1932

Genetics of the Protozoa, in relation to some of the greater problems of genetics. Japanese Journal of Genetics, 8(2–3):66–84.

Heredity and environment in pediatrics. In: *Practice of Pediatrics,* by J. Brennemann, vol. 1, pp. 1–28. Hagerstown, Md.: W. F. Prior Co., Inc. Reprinted in 1937, 1942.

With D. Raffel, Ruth S. Lynch, and T. M. Sonneborn. The diverse biotypes produced by conjugation within a clone of *Paramecium aurelia.* J. Exp. Zool., 62(2):363–408.

1933

Originality in the development of life. Yale Review, 22(3):559–72.

Thomas Hunt Morgan, Nobel Laureate. Sci. Mon., 37:566–67.

The Universe and Life. New Haven: Yale Univ. Press. 94 pp.

1934

General biology and genetics. In: *The Problem of Mental Disorder,* ed. by M. Bentley and E. V. Cowdry for the National Research Council, pp. 216–26. New York: McGraw-Hill Book Co.

1935

Genetics. New York: W. W. Norton & Co., Inc. xiii + 366 pp. (*Problems,* pp. 367–421, a supplement to the above volume, was issued separately by W. W. Norton & Co., Inc.)

Genetic Variations in Relation to Evolution. Princeton: Princeton Univ. Press. 138 pp.

1936

Fundamental units in biology. Science, 84(2186):445–50.

With T. M. Sonneborn. Relation of endomixis to vitality in *Paramecium aurelia.* Comptes rendus du XIIème Congrès international de Zoologie, 1935, pp. 416–20. Lisbon: Casa Portuguesa.

1937

Biology and social reform. Journal of Social Philosophy, 2(2):155–66.

Formation, inheritance and variation of the teeth in *Difflugia corona.* A study of the morphogenic activities of rhizopod protoplasm. J. Exp. Zool., 77:287–336.

1938

Sex reaction types and their interrelations in *Paramecium bursaria*. I. Proc. Natl. Acad. Sci., 24:112–17.

Sex reaction types and their interrelations in *Paramecium bursaria*. II. Clones collected from natural habitats. Proc. Natl. Acad. Sci., 24:117–20.

1939

Genetics of *Paramecium bursaria*. I. Mating types and groups, their interrelation and distribution; mating behavior and self sterility. Genetics, 24:202–33.

Mating types and their interactions in ciliate Infusoria. Introduction. Am. Nat., 73:385–89. Also in Biol. Symp., 1:117–21 (1940).

Mating types and their interactions in ciliate Infusoria. *Paramecium bursaria*. Am. Nat., 73:414–31. Also in Biol. Symp., 1:146–63 (1940).

Senescence and death in Protozoa and invertebrates. Chap. 2 in: *Problems of Aging; Biological and Medical Aspects,* ed. by E. V. Cowdry, pp. 32–52. Baltimore: Williams & Wilkins Co. 2d ed., 1942.

1940

Cytology of ciliate Protozoa, in particular, the chromosomes and their behavior at conjugation in *Paramecium bursaria* and in other species of Paramecium; also the chromosomes in the Opalinidae. In: *American Philosophical Society Year Book,* pp. 246–49. Philadelphia: The Society.

Chromosomes and cytoplasm in Protozoa. In: *The Cell and Protoplasm,* ed. by F. R. Moulton, pp. 44–55. Publication no. 14, American Association for the Advancement of Science.

The beginnings of social behavior in unicellular organisms. Science, 92:539–46. Also in Leidy Memorial Lecture, University of Pennsylvania Bicentennial Conference, pp. 1–17 (1941).

1941

Genetics of *Paramecium bursaria*. II. Self-differentiation and self-fertilization of clones. Proc. Am. Philos. Soc., 85:25–48.

Hereditary status of the rhizopods. Symposium on *Cytology, Genetics and Evolution,* pp. 67–79, University of Pennsylvania Bicentennial Conference. Philadelphia: Univ. of Pennsylvania Press.

Inheritance in Protozoa. In: *Protozoa in Biological Research,* ed. by G. N. Calkins and F. M. Summers, pp. 710–71. New York: Columbia Univ. Press.

The laws of heredity and our present knowledge of human heredity on the material side. Chap. 1 in: *Scientific Aspects of the Race Problem,* pp. 1–73. New York: Longmans, Green & Company, Inc.

Some aspects of the biological bases of human nature. In: *The University and the Future of America,* pp. 89–107. Stanford: Stanford Univ. Press.

The transition from the individual to the social level. Science, 94(2446):447–53. Also in *Levels of Integration in Biological and Social Systems,* ed. by Robert Redfield, Biol. Symp., 8:105–20. Lancaster, Pa.: Jacques Cattell Press.

1942

Genetics of *Paramecium bursaria.* III. Inheritance of mating type, in crosses and clonal self-fertilization. Genetics, 27:193–211.

1943

Raymond Pearl. 1879–1940. In: National Academy of Sciences, *Biographical Memoirs,* 22:295–347.

1944

Changes in the surrounding medium produced by free-living cells. In: *Colloid Chemistry,* ed. by Jerome Alexander, vol. 5, pp. 1162–74. New York: Reinhold Publishing Corporation.

With Pauline Opitz. Genetics of *Paramecium bursaria.* IV. A fourth variety from Russia. Lethal crosses with an American variety. Genetics, 29:576–83.

Paramecium bursaria: life history. I. Immaturity, maturity and age. Biol. Bull., 86(3):131–45.

Paramecium bursaria: life history. II. Age and death of clones in relation to the results of conjugation. J. Exp. Zool., 96:17–52.

Paramecium bursaria: life history. III. Repeated conjugation in the same stock at different ages, with and without inbreeding, in relation to mortality at conjugation. J. Exp. Zool., 96:243–73.

Paramecium bursaria: life history. IV. Relation of inbreeding to mortality of ex-conjugant clones. J. Exp. Zool., 97:165–97.

1945

Social life and interrelationships in certain Protozoa. Sociometry, 8(1):9–20.

Paramecium bursaria: life history. V. Some relations of external conditions, past or present, to aging and to mortality of exconjugants, with summary of conclusions on age and death. J. Exp. Zool., 99:15–31.

1946

Stirring days at A. and M. Southwest Review, 31:341–44.