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OSCAR RIDDLE

1877—1968

A Biographical Memoir by

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Biographical Memoir

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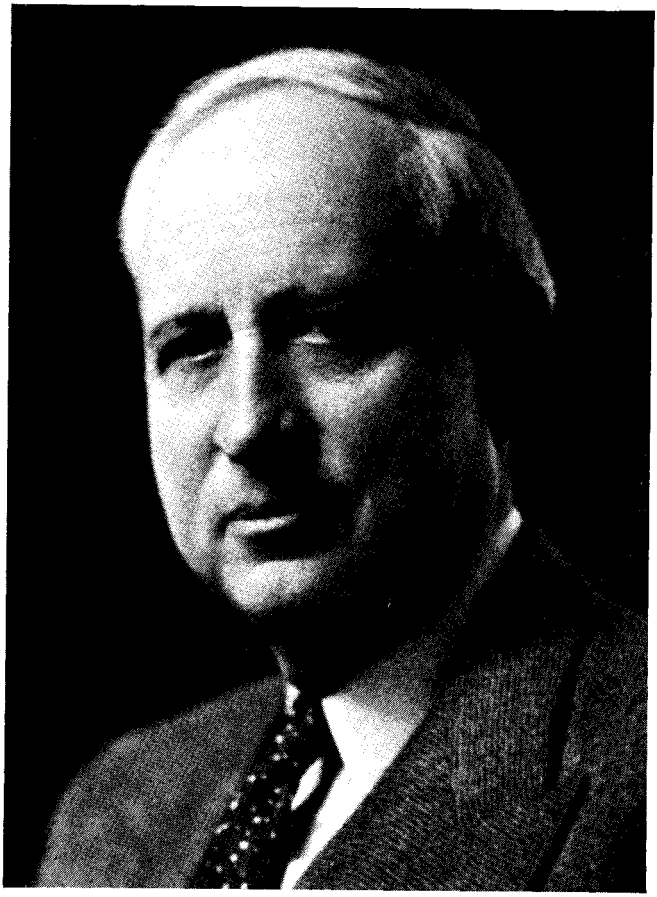

Oscar Riddle

OSCAR RIDDLE

September 27, 1877–November 29, 1968

BY GEORGE W. CORNER

OSCAR RIDDLE, zoologist and proponent of the freedom of science teaching, was born September 27, 1877, in Greene County, Indiana. His birthplace was a log house near a village called Cincinnati, twenty miles from the university town of Bloomington. His boyhood in this countryside of heavily wooded hills and narrow valleys is well described in autobiographical notes Riddle prepared for the files of the National Academy of Sciences. The first part of the present account of his life, scientific career, and writings largely follows his own narrative.

Oscar Riddle's father, Jonathan Riddle, came from a North-of-England family that had settled first in Virginia. On his Indiana land he made a comfortable living by farming and breeding livestock, though always with the narrow economic margin characteristic of pioneer life. He kept a racehorse and was an enthusiastic hunter of deer, wild turkey, and the bears that were then to be found in the hills of Indiana and neighboring states. It is of interest, in connection with his son's attitude toward dogmatic religion, that Jonathan Riddle was never active in any religious sect.

Oscar's mother, Amanda Emeline Carmichael, was born at Cincinnati, Indiana, of Scottish and northern Irish ancestry. Her father, relatively prosperous among the villagers, kept a

general store and a flour mill. Something of a philosopher, Mr. Carmichael wrote a number of unpublished essays, well worded (according to his grandson) and showing deep interest in the question of free will and similar religiophilosophical topics. Sometimes, in the absence of the local Baptist preacher, he took the pulpit and preached sermons appreciated by the congregation.

Jonathan Riddle died in 1882 at the age of fifty-five, leaving nine children of whom the youngest was six months old. His wife, then forty-five years of age, raised all of them to maturity and lived on to the age of eighty-nine. Although during her husband's lifetime she professed no religious faith, after he died she joined the local Baptists, often remarking, however, that she did not believe in eternal punishment nor did she think it sinful not to be a professed Christian. Her husband's death left the family in straitened circumstances, and all the older children had to help with the farm work. In his written reminiscenses Oscar gives a graphic account of his early boyhood and schooling.

"In our home, and on our farm, there was much work for even the smallest hands to do. Drinking water had to be carried up a steep hill from a cold, fast-flowing spring 60 or 70 yards away; and in summer, to and from the milk-house at this spring all the milk, some fruits, and vegetables were carried. Each winter and spring some acres had to be cleared of forest; later a variety of crops had to be planted and this rough and stubborn terrain had to be cultivated and harvested.

"In order to obtain some money, it was necessary for the sons of our family to obtain work on nearby farms or in stores. Thus during all of my ninth and tenth years, except for the short term of school, I supported myself by work on a farm two miles from my home."

Oscar Riddle's first school, a one-room cabin, was a mile from the Riddle farm by way of a narrow path through woods

and across fields. Like other boys of the neighborhood, Oscar walked barefoot, even in frosty weather, wearing boots only when snow lay on the ground. The school term was brief, about seventy days in each year. After two years at the country school, Oscar attended school in the village, with somewhat longer terms, as much as one hundred days. To attend school and such events in the village as spelling bees, debates, and church suppers, the Riddle children walked two miles each way.

When twelve years old, Oscar helped in a store and delivered newspapers; at thirteen he trapped furbearing animals in wintertime; and for two years he swept the schoolroom floor and built the fire, for ten cents a day. From his fourteenth year he not only supported himself year-round, but like his older brothers was able to turn over a little money to his mother.

Through hunting and trapping Oscar developed his lifelong interest in the habits of birds and mammals. As early as the age of eight his curiosity had been awakened by fossil shells and imprints he had noticed in the banks and gullies around his hillside home. These shapes in sandstone and limestone, he was told, represented animals of kinds that lived only in the sea.

"This seemed to indicate, and led me to suspect, that our earth must be very old. Yet all the preachers I had heard insisted, and cited the Biblical record in support, that the earth was created about 6,000 years ago, and that there had been one—and only one—big and short-lived flood. How could this flood have brought animals to our high hill from a sea that is almost a thousand miles away? Even more disconcerting to me were the dicta of these preachers, again supported by a Heaven-born Bible, that a hot Hell exists, and that after death all unbelievers go there and burn everlastingly. And I had to regard myself as such an unbeliever!"

This conflict between dogma and observed fact caused the boy great distress of a kind not uncommon in those days in youngsters whose inquiring minds were breaking away from the

rigid beliefs of their elders. From the age of ten until he was thirteen, Oscar tells us, the threat of hellfire often wrung a prayer from him and brought frightened tears to his pillow before he slept at night.

These fears were suddenly brushed away one night when the boy attended a lecture at the village church, the very place where he had so often heard the threat of damnation. A college mate of his elder brother, named Francis Price, was studying zoology at Indiana University under a twenty-seven-year-old professor, Carl H. Eigenmann, who later became a member of the National Academy of Sciences. Price had arranged to give a talk at the church on the evolution of living things and to illustrate it borrowed from Eigenmann a collection of fishes preserved in alcohol, chosen to illustrate the principles of adaptation and natural selection. Either Price was very bold for the time or the current pastor was more liberal than those Oscar had heard earlier. At any rate the lad was so thrilled by the talk that he had Price invited to the Riddle house for the night. Thus enabled to examine the wonderful specimens for himself, with Price's kindly guidance, he understood the relics of ancient life in the hillside strata that had worked so powerfully upon his youthful mind. "I never prayed or wept upon my pillow again," he wrote in old age. "Nothing in a long life has equaled the release, thrill, and resolution obtained from this message, so simply delivered by a young man from a neighboring farm."

After completing grade school in the village of Cincinnati, Oscar Riddle attended high school in Bloomfield, the county seat of Greene County, and entered Indiana University in the spring of 1896. He began at once the formal study of biology and spent two summers at the university's biological field station, then at Turkey Lake, Indiana. In the summer of 1899 his good work on a survey of Winona Lake led Professor

Eigenmann to recommend him to the U.S. Commissioner of Fisheries for assignment to collect tide-pool and freshwater fishes of Puerto Rico, which had just become a possession of the United States. Taking a hasty course in Spanish, Riddle interrupted his college work and left for Puerto Rico in the autumn of 1899. The island's Commissioner of Education promptly asked him to teach biology to students of pharmacy and of education in the newly established Model and Training School at San Juan. Early in 1900 he also took over a beginning class in chemistry.

That summer he was one of five men chosen to conduct teachers' institutes in the ten largest cities of Puerto Rico. By this time he was able to lecture in Spanish. Traveling by railway, horse-drawn carriage, ox cart, and steamer, he covered much of the island and the neighboring smaller isle of Vieques. During a second year at San Juan Riddle taught classes in biology in the high school, some of them in Spanish, and followed up his course in chemistry for pharmacy students by teaching them zoology and physiology. Several of his class of fourteen, he learned years later, became physicians, one a lawyer, one a banker, another a legislator, and one a professor of Spanish in the new University of Puerto Rico. All this teaching had left but little time for zoological collecting, but in 1901 Riddle, at his own expense, made a summer's scientific expedition to the delta of the Orinoco River, south of Trinidad.

Returning home in the autumn of 1901, he registered at Indiana University for the final year required for his bachelor's degree. In January and February 1902 he accompanied Carl Eigenmann on a six-week trip to collect blindfishes (a special interest of Eigenmann's) in the caves and underground streams of western Cuba. During that year also he prepared an article on the fishes he had himself collected in Venezuela and Trini-

dad, but the manuscript that would have yielded his first publication in zoology was stolen from him. He sold his collection to the Field Museum in Chicago.

After graduation from college Riddle declined a generous offer from a family friend of a mercantile position in Indianapolis. He also declined a teaching post at the University of the Philippines and instead enrolled as a graduate student in the University of Chicago. There he was under the general leadership of Charles O. Whitman, but also followed (as he had hoped) the lectures of Jacques Loeb. His plan was to prepare himself for teaching and research, aiming for a career on the preclinical side of a medical school. In his first term he took Loeb's radically planned course in physiology, or rather general physiology as we would term it today. Although Riddle does not say so, it is obvious in retrospect that Loeb's departure that winter for the University of California was an intellectual loss to the young man, who could have benefited much if he had gone on to research under Loeb, from the latter's rigorous analytical thinking, of a kind that the still largely descriptive methods of zoology did not demand.

Riddle's postgraduate training was interrupted by his appointment in the spring of 1903 to teach physiology in Central High School of St. Louis, Missouri. Loeb's department had been asked to recommend a man capable of introducing laboratory work into their didactic course. The project interested Riddle, who moreover needed money to help a sister go to college in St. Louis. He spent altogether five half-year periods there (1903–1906) interspersed with other activities, including participation in the summer course in physiology at Woods Hole in 1903, a summer assistantship in zoology and biology at Indiana in 1904, and a similar post at Indiana for eight months in 1905 while on leave of absence from St. Louis. At St. Louis he was also principal of one of the city's evening schools and

filled in what was left of his working hours by studying French and German at the local Berlitz school.

In February 1906, Riddle resigned his St. Louis post and returned to Chicago to complete his postgraduate studies while resuming his assistantship in zoology. He found Loeb's successor in the chair of physiology, G. N. Stewart, less sympathetic to the kind of training he wished to obtain than was Professor Whitman and therefore decided to make zoology, under Whitman's tutelage, his major subject for the doctorate. Even though he had accumulated sufficient credits for a minor in physiology, with Whitman's approval he chose biochemistry under Albert P. Matthews as his designated minor subject.

Whitman put him to work for his doctoral dissertation on a problem of considerable theoretical importance, the cause of the alternation of light and dark bars seen on the feathers of many kinds of birds, notably fowl and pigeons. Whitman's own long studies of the evolution of birds, and especially of their color patterns, had brought him face to face with this question, which, as he perceived, called for both genetic and biochemical studies. Thus was the course of Riddle's career as an investigator set by the time he took his Ph.D. in zoology, in June 1907. The guidance and companionship of Whitman, he says in his autobiographical statement, provided one of the most profitable and delightful epochs of his life: "Whitman became nearer to being a father to me than anyone I have known."

After taking his doctorate, Riddle remained at the University of Chicago as an associate (a rank between assistant and instructor) in zoology and embryology and also as an assistant in experimental therapeutics (a research post). The next year he was promoted to instructor in zoology and embryology, and in the following two years he twice gave the course in embryology for medical students and organized new courses in vertebrate zoology and general biology and a graduate course in the

physiology of development, a quite novel topic. From his laboratory he published several papers on color formation in feathers, the development of yolk in hens' eggs, and the rate of digestion in cold-blooded animals. In July 1910, he obtained leave of absence for a year of travel and study in Europe. Whitman had assured him that upon his return he would be made assistant professor of biology and given charge of two of the three terms of the introductory course in zoology.

Riddle began serious work abroad by settling for a few weeks in Berlin, where in the university library he wrote a paper on melanin formation in feathers, which he presented at the Eighth International Zoological Congress, at Graz. After the Congress he visited various European countries as a tourist. In Frankfurt he called on Paul Ehrlich, who advised him about intravitam stains for studying oxidation and reduction in animal tissues, a topic he intended to investigate in the autumn at the Naples Zoological Station.

Riddle had not been long at Naples when he received the distressing news of Whitman's death on December 6, 1910. It can do no harm now to the memory of the distinguished personages upon whom Riddle's career depended at that critical time to say that Whitman's death was very unfortunate for him. Frank R. Lillie of the Chicago department of zoology, who had regarded himself as Whitman's heir apparent and in fact succeeded to the senior chair, was planning a radical redisposition of the staff. Lillie wrote to Riddle in January 1911 that there was internal opposition to him (as indeed there had been to Whitman) and that he would not be reappointed. At about the same time Whitman's friends in the university wrote of their fears that the late professor's extensive unpublished researches on the evolution of pigeons would never be published under the new regime. Riddle, therefore, with self-sacrificing loyalty to his late chief and mentor, left Naples and went home to see what could be done to salvage Whitman's lifework. The

struggle to take on this task, he records, and the labor of completing it were more formidable than any other efforts of his lifetime.

Albert P. Matthews, Professor of Biochemistry, managed to get him a six-month appointment on the payroll of the Laboratory of Experimental Therapeutics, a research unit of Matthews's department. The Sprague Institute gave him $300 toward the expenses of maintaining Whitman's large breeding colony of pigeons, which was still kept at the late professor's home.

In 1912 came a great step forward in Riddle's career when the Carnegie Institution of Washington made him a salaried research associate, with funds to continue the pigeon colony, and undertook to pay for publishing the Whitman papers whenever they might be ready for the press. Late in 1913 Riddle moved, with the birds and the manuscripts, to the Carnegie Institution's Station for Experimental Evolution, at Cold Spring Harbor, Long Island. This appointment must have been initiated by Charles B. Davenport, founder in 1904 and director of the station. Yet Riddle states in his autobiographical notes that he had a constant struggle to obtain adequate quarters for his birds and efficient laboratory space for himself and indeed received little encouragement for his research until, after many years, Albert F. Blakeslee and later Milislav Demerec succeeded to the directorship.

Davenport's coolness toward Riddle arose, no doubt, not only from differences of temperament, but also from Riddle's devotion to the memory of Whitman, whose scientific ideas as revealed in the documents that his disciple was editing were deeply at variance with those of Davenport. The research program at Cold Spring Harbor was based on the Mendelian principles that, since their rediscovery in 1900, had revolutionized genetics. Whitman, on the other hand, had remained unresponsive to much of the new genetics. He had begun to study evolution in birds in 1892, at the age of fifty, under the

influence of an older school of biological thought. To him recapitulation was the central fact of heredity; and he had, moreover, chosen as the hereditable factors to be studied in his hybrid birds three that did not lend themselves easily to Mendelian analysis: color patterns, which are exceedingly complex in birds, and sex determination and fertility, which are complex phenomena in all animals. He had never accepted the Mendelian ideas of unit characters and genetic dominance; he doubted the importance of mutations for evolution and declared that he had found evidence for evolution by orthogenesis. The presence in Davenport's laboratory of an outspoken, enthusiastic pupil of an anti-Mendelian must have irked the sensitive spirit of its director.

At any rate, Riddle, while organizing, against what he felt to be his chief's indifference, a laboratory that never quite matched his own standards and getting under way a broad program of research, toiled on and on with Whitman's voluminous and, to a large extent, ill-sorted papers. The task was varied and immense, requiring rearrangement and assemblage of misplaced portions of chapters, analysis of numerous tables, and placement of numerous illustrations. In this task also he did not get all the help he needed, for Mrs. Whitman had for reasons of her own at times limited his use of the materials. At last, in 1914, the Carnegie Institution published the Whitman papers in three large and handsomely illustrated volumes. The first two, edited solely by Riddle, present a clear statement of Whitman's studies on natural and hybrid pigeons and doves, their growth, and particularly their inheritance of feather patterns. In the third volume Riddle gathered together Whitman's intensive observations of sex behavior and reproductive activities. Feeling himself not competent to assess this material, he turned the detailed editing over to Harvey A. Carr, Associate Professor of Psychology at the University of Chicago. This third volume, largely free of the conjectural and controversial bias of

the first two, is of more permanent value. It gave Riddle the physiological background of much of his experimental research.

Oscar remained at Cold Spring Harbor through the whole of his active scientific career, as a member of the Carnegie Institution's Station for Experimental Evolution, later called the Department of Genetics. It seems a pity that he was not in a teaching institution, for with his love of nature, his cordial outgoing manner, and his enthusiasm for the study of grand problems—inheritance, metabolism, and sex determination—he would have been an admirable college professor of biology. As it was, he worked away in relative intellectual isolation in his own laboratory, with an assistant or two, on a research program not intimately related to the studies on chromosomal and statistical genetics that interested his chief, C. B. Davenport, and the rest of the staff. He was largely out of contact with young people whose minds he might have awakened, as indeed he had done during his brief stay at the University of Puerto Rico and in St. Louis.

Life in the semirural ambience of Cold Spring Harbor well suited this country-bred man, who came to love the wooded slopes of Long Island's North Shore, where gentle streams glide through ponds and marshes down to tidal harbors and the broad salt waters of the Sound, and where the songs of forest birds and the mewing of seagulls mingled with the cooing of his caged pigeons. Long remaining a bachelor, Oscar had a room in the plain old country house that Davenport had adapted as a dormitory for the unmarried assistants. Most of the year his daily circuit took him to his nearby laboratory and back in the evening, with only an occasional visit to New York City, thirty miles away. From June to August life was somewhat more varied. Davenport had kept up, along with his Carnegie department, the summer courses of the Long Island Biological Association, from which the whole station had grown. Students and summertime investigators of marine life came to live on the

grounds, and with them Oscar enjoyed an after-supper game of softball. Now and then on Saturday afternoons he could be seen with his stocky form and merry round face driving off with a carfull of the girl assistants—there was safety in numbers—for sea-bathing at Jones Beach on the South Shore. Occasionally, he invited one of the visiting biologists to a seafood dinner at a shore hotel, followed by a good talk on scientific matters and a moonlight swim. The writer of this memoir recalls one such evening when the water of the Sound was silver-smooth at slack tide under the August moon. Oscar, who was a chain smoker, lit a fresh cigarette before launching himself upon the salt water and then, swimming on his back in order not to douse his smoke, drifted out toward the open Sound, where all that could be seen of him in the moonlight was a bobbing shadow and the faint gleam of his cigarette.

At the outbreak of World War I, a company of the Home Guard of New York State was formed at Cold Spring Harbor. Oscar joined up as a private, but soon rose to the rank of sergeant and finally arrived at a first lieutenancy. In 1918 he achieved more serious military status when he was commissioned captain in the Sanitary Corps of the Army and served as nutrition officer and on related assignments at Fort Oglethorpe, Camp Meade, and overseas at Dijon and Bordeaux.

Back at Cold Spring Harbor after the war, Oscar's researches kept him busy, as before, through the summer months; therefore, he took short winter vacations, usually Caribbean cruises. One of these holiday voyages altered his way of life, for in 1937 at the age of sixty he astonished his friends by marrying a lady whom he had met on the previous winter's cruise. Leona Lewis, like himself a Midwesterner but some years younger than he, had been a school and college teacher of music in Iowa and Oregon, and during the depression years of the early 1930's was a supervisor on the Governor of Indiana's Relief Commission. As Oscar wrote of her after many years of marriage, she was

"trained, industrious, beautiful, and able." Their friends would add that she was a very agreeable and hospitable hostess.

With his wife, Oscar settled down to contented domestic life in a commodious apartment occupying the first floor of a large old mansion, near the laboratory, that had been bequeathed to the Carnegie Institution by a wealthy New Yorker. There, in their spacious living room, Oscar and Leona loved to have dinner guests join them in a favorite game, reminiscent of their shipboard pleasures. The carpet, rolled back, revealed a shuffleboard diagram that Oscar had painted on the hardwood floor. Cues and disks were brought from a closet, and professional concerns were set aside as the guests, however dignified and eminent in the academic world, joined in an evening of simple party fun.

In Riddle's scientific career one achievement in particular stands out. This was the preliminary isolation, naming, and study of prolactin, the hormone of the pituitary gland that stimulates the mammary gland to produce milk. This work will be discussed later. As to the long and laborious studies to which he devoted most of his life, on the formation and inheritance of feather patterns, and on the nature, the inheritance, and the reversibility of sex, it must be said that, although he contributed numerous original observations, his general conclusions have largely been superseded.

A prefatory explanation is here urgently called for. Riddle boldly attacked broad general problems of animal life, of long concern to naturalists and zoologists, at a time when physiology and biochemistry were rapidly coming forward to supplement or supplant the older methods of morphology. It was tempting and all too easy to formulate biochemical and metabolic hypotheses to explain such mysteries as sex differentiation and the inheritance of color patterns. Riddle himself perceived in later years that some of his conclusions had been premature. "Fate or fortune," he wrote, "led me into two fields which were

both of them in a stage best defined as quite exciting, rapidly changing, and beset with vast uncertainties. During this early period I made some lasting contributions to these two subjects; but my inexperience led me to an overconfidence and dogmatism which more mature years could only regret."

In an early paper on a supposed metabolic cause of sex differences in pigeons, based on some of Whitman's conclusions, Riddle relied too much, he later said, on impressions obtained from conversations with Whitman. Two self-admitted defects, dogmatism and overreliance on uncertain authority—oral and written—did not altogether disappear from his thinking even in more mature years. There would be no point in reviewing here in detail Riddle's voluminous research publications. To place his work, as far as can now be seen, in context with the biology of his time, we need only summarize his findings, according to the major topics that he himself listed in the autobiographical sketch referred to earlier.

Riddle's early effort to explain a prevalent special form of "barring" (i.e., alternating stripes of light and dark color) in the feathers of highly pigmented birds led to the conclusion that this pattern is produced by daily variation in the rate of formation of dark pigment (melanin), caused by a diurnal metabolic rhythm. Later studies of B. H. Willier have shown that the rhythm of pigment deposition is by no means as regular or as rapid as Riddle thought, and that its fluctuation is brought about by special cells known as melanocytes, the bar gene of which acts upon the biochemical mechanism of melanin formation in an "on and off" sequence.

Riddle devoted years of detailed physiological and biochemical research to the question of sex determination, concluding that maleness and femaleness depend directly upon a difference in the rate of basal metabolism, beginning in the ovum. This hypothesis was promptly questioned by geneticists, and today it is clear that sex differentiation is brought about by

the balance of male- and female-determining genes. A difference between the basal metabolism of the two sexes is simply one of many effects of differing sex-chromosome control.

Carrying forward a study of sex reversal and hermaphroditism in hybrid pigeons, begun by C. O. Whitman, Riddle explained these aberrant phenomena as special cases of metabolic imbalance; subsequent investigators have shown that they result, in a complex manner, from genetic and endocrine causes. A remarkable side-product of Riddle's study of hermaphroditism, his establishment by selective breeding of a race of hermaphrodite-producing pigeons, is in fact difficult to reconcile with a metabolic theory of sex.

In Riddle's middle years, when endocrinology was barely getting under way, the reproductive cycle of higher animals was a highly mysterious phenomenon. Whether the cycles of ovulation, estrus, and menstruation (in primates) are regulated by the nervous system or the endocrine glands was a central problem. Riddle's work with birds led him to side, correctly, with those who spoke for the endocrine system. Experiments of his own, on which he laid great stress, purporting to demonstrate the existence of a hormone of the thymus gland ("thymovidin") responsible for the cyclic formation of the egg albumin, the activity of the shell gland, and deposition of the shell, have not been confirmed.

In the course of these studies of sex differences, reproductive cycles, and metabolism in pigeons, Riddle with extraordinary energy and persistence had tried every means he knew and could find in the literature to test his hypotheses by measuring the physiological and biochemical states of his birds. By 1939, when he had largely shifted his attack to other problems, he with his associates had published scores, even hundreds of journal articles and had compiled no less than 800 tables of quantitative experimental results—so many, in fact, that he could never get them published as a whole. In the late 1920's and early 1930's

Riddle used his great experience in the handling of pigeons in joint studies, with F. G. Benedict of the Carnegie Institution's Nutrition Laboratory, of the normal basal metabolism of pigeons and ringdoves and its variation under changing conditions of temperature, season, and endocrine balance.

For many years, in pursuance of his interest in evolution, Riddle carried on continuous breeding experiments aimed at demonstrating the production of distinctive races of ringdoves by selection followed by inbreeding of birds descended from a heterogeneous popoulation. In a monograph published in 1947, he reported having established several races characterized variously by large or small thyroid glands, long or short intestinal tracts, early or late sexual maturity of females, production of large or small eggs, and similar traits. Such artificial evolution differs from that carried on for millenia by practical breeders of domestic animals and plants only in that it was done with a scientific aim and advanced knowledge of genetic processes. It thus adds some little additional support for the concept of natural selection as a major factor in the production of races and species. Other biologists, for example, W. E. Castle, E. Carleton McDowell, and Fernandus Payne, had accomplished similar genetic selection of morphological characters; the novelty in Riddle's work was that most of the characters he succeeded in establishing were physiological.

Riddle's reputation as a scientist will in the long run no doubt rest chiefly on his pioneering chemical and physiological study of the pituitary mammatropic hormone, which he was the first to isolate in a form approaching purity and to which he gave the name "prolactin." Various experimenters from about 1905 on, seeking to find the cause of lactation, variously and unconvincingly ascribed it to the placenta, the corpus luteum, and the estrogenic hormone of the ovary. In 1928, however, P. Stricker and F. Grueter of Strasbourg announced that they

had induced lactation in rabbits by injection of aqueous extracts of the anterior lobe of the pituitary gland. These investigators erroneously believed, however, that previous preparation of the mammary gland by the hormone of the corpus luteum was necessary for milk production. The writer of this memoir, working at the same time as the Alsatian scientists, but unaware of their studies, reported in 1930 experiments that convincingly showed that alkaline aqueous extracts of the anterior pituitary will cause active secretion of milk in spayed rabbits that had never ovulated. My attempts to purify the lactation hormone, however, completely failed even with the collaboration of a biochemist. We were unable to proceed beyond the preparation of a crude aqueous extract.

Riddle apparently did not know of Stricker's and Grueter's work on pituitary-induced lactation, but he read the article of Corner (1930) and was stimulated to investigate the subject himself. He was already an experienced endocrinologist, having been the first to use insulin, thyroxin, adrenalin, and pituitary gland extracts in metabolic studies on pigeons. With two associates, R. W. Bates and S. W. Dykshorn, he produced a highly (though not completely) purified lactogenic substance that he named prolactin and separated it from other hormonal substances sufficiently to indicate its independent status. This work was published in 1932. Riddle and his associates, Bates and E. L. Lahr, soon identified the substance as a protein. In the course of these biochemical studies, he made the remarkable discovery that the secretion of crop milk in the pigeon is induced by a pituitary hormone which he identified with prolactin as soon as he had the latter in relatively pure form. The growth of the pigeon's crop thus produced may readily be used, as Riddle pointed out, as a convenient, rapid, and relatively economical method of testing the lactogenic action of pituitary extracts. The crop gland test of Riddle was very soon applied to

further purification of prolactin by W. R. Lyons at Berkeley and finally to its preparation in crystalline form by Abraham White and associates at New Haven.

Although Riddle spent all but the first years of his scientific career in an advanced research institute, he never lost interest in the elementary teaching of biology. His first published paper (1906) dealt with that subject and appeared in a journal of secondary education. For the next thirty years he pondered the subject in the light of his own boyhood experience of intellectual liberation through biological study and came more and more to blame the weakness of biology in the high schools on the antievolutionary pressure of dogmatic religious groups.

His feeling finally boiled over in an address at St. Louis on January 1, 1936, as a vice president of the American Association for the Advancement of Science and chairman of its section on zoology. Under the title, "The Confusion of Tongues," he eloquently contrasted the recent rapid development of the life sciences in American universities and colleges with the concurrent virtual suppression (as he saw it) of the essential evolutionary contents of these sciences in the high schools by religious dogmatism. Widening the scope of his address, he went on to a critical examination of supernaturalism in general. To speak as he did was, under the circumstances, quite bold and indeed indiscreet had not his position in an independent nonteaching institution protected him from the attacks of dismayed clerics and parents. The address naturally attracted nationwide attention. *The New York Times* printed much of it on the day after its delivery, and within the month *Science* published it in full in two installments. Riddle was inundated by several hundred letters of approval and condemnation.

The then-president of the Union of American Biological Societies, E. V. Cowdry, was in Riddle's audience at St. Louis. Impressed by the address, he asked Riddle to organize and preside over a committee to examine the current state of biology

teaching. After some years' study of the high schools the committee published in 1942 a report largely confirming Riddle's charge of religious restraints upon the teaching of evolutionary theory.

Feeling that his own ideas and the committee's report deserved a wider audience, Riddle went to work in 1947 on a book, *The Unleashing of Evolutionary Thought,* and after four years had the manuscript ready. Ten prominent publishers, including a university press, one after another rejected it. Turning to a publisher of the "vanity press" type, who put out books subsidized by their authors, Riddle finally got his work in print in 1954. He blamed the repeated rejections on the timidity of publishers with regard to his antireligious position and ascribed the book's small sale and the scanty attention given to it, when published, by general and scientific reviewers, to inadequate advertising by the publisher. Actually, the volume did not effectively represent his wide information and humane ideas. Its outward appearance was unimpressive, its contents heavy and discursive. The first one hundred fifty pages, however, present a thorough and clear review of current thought about human nature and evolution. That part of the book, if separately published, lightened by a bit of the humor Riddle could exhibit in conversation, somewhat less belligerently antireligious, and attractively illustrated, might have been accepted by thoughtful general readers as a valuable statement of contemporary scientific humanism.

Two excerpts will show something of Riddle's personal thought on great problems of human duty and fate. The first can be recommended to both sides in the current discussion of "women's liberation."

"A unique thing about the abstract quality called sex is that it is observed and known only in terms of differences between two unlike types. In an all-male or an all-female world, our concept of sex could never arise. But once the idea and fact of

sex difference was recognized by man, it became a dividing line between the two chief groups into which all humans are classified by themselves and by others. And here, indeed, there is no doubt of human biological inequality. To this contrast of bodily form and function, however, nature herself seems content to assign mainly unlike and unequal shares in reproduction and in a few diseases; meanwhile, and in addition, humans themselves have assigned to sex almost everything on earth and in heaven. In the numerous cultures of our own day—barbaric and civilized—there is scarcely a category of performance that is not apportioned on a basis of sex. To round out this absurdity, the apportionments of one culture contradict those of another.

"Just as the idea of, and the wish for, progress is either unknown or quite new among men, a declared and purposeful search for sound and unexplored ways of developing and utilizing the special qualities of each of the two sexes—and especially those of the female sex—is yet to be attempted in any culture anywhere. It is true, of course, that bars and taboos are being lifted in many countries; but tradition, masculine vanity, law, custom and religion all compete for rule within this exceedingly broad area. The divisive aspect of sex usually still has right of way over any concerted effort to exploit the rich possibilities of what can be made of two rather similar genetic endowments that are so flavored as to yield two (often) superb and complementary personalities."

Another passage presents Riddle's answer, as a biologist, to the question of individual immortality. After discrediting orthodox views and deploring a stagnation of literature that he thought resulted from them he writes,

"The boundaries of reality are indeed quite different from those of most bygone human imagination—of stretched and misty hope. Nevertheless, firm truth from biology and sociology now assures that two forms of near-immortality for man hover or hide on natural creation's crest: the same biological thread

that saved for man the gains of a dim past ties also his own genes to a lineage that may end only with highest life on earth. And personal social worth puts its benign leverage upon the unborn tomorrows. Clearly, the countless blessings of our times point backward to uncounted personalities. A Lincoln or a Jefferson is gripped lightly by a grave, but firmly by a durably spreading society."

In the second part of *The Unleashing of Evolutionary Thought* Riddle attacks directly the opposition of dogmatic religion to the teaching of evolutionary theory, upon which he based such hopes for mankind as those suggested in the foregoing excerpts. The section is a vigorous polemic that may profitably be reread by anyone investigating the socioreligious state of our country in the 1940's. The book ends with a collection of comments, favorable and unfavorable, on Riddle's St. Louis address of 1936 and a final chapter predicting a continuing but ultimately victorious struggle, in the western world, of naturalism against supernaturalism.

Distressed but not discouraged by the slight impact of this heartfelt and laborious book, Riddle continued to publish his opinions on science and religion in a way he could handle more effectively, in articles in such journals as *The Humanist, The Rationalist, The Realist,* and *The Age of Reason.* Almost every year until 1967 this indefatigable fighter for rational thought and education brought out one or more papers on evolution and the need for unhampered teaching of biology.

In 1945, after Riddle reached the Carnegie Institution's stated age of retirement, he and his wife bought a house and five acres of land near Plant City, Florida, where he contentedly carried on his study and writing in the fields that had long interested him. After his book of 1954 was off the press he made several trips on invitation to lecture and lead seminars, at colleges all over the country, on endocrinology and the biology of reproduction. In 1959–1960 he was president of the American Rationalist Federation. In 1961, stimulated by cer-

tain criticisms of his published work on the role of prolactin in reproductive behavior of birds, he devoted much time to writing articles reviewing and defending his conclusions on that subject.

Riddle's lifelong good health began to break down in 1964, when at the age of 87 he suffered a mild coronary occlusion. Other illnesses followed, and in 1966 he was found to be suffering from an inoperable carcinoma of the prostate gland, which ended his life in 1968. His wife Leona died a few weeks later; there are no surviving close relatives.

Oscar Riddle's outgoing disposition, his enthusiasm for research, his broad view of biological processes, and his valiant fight for humane consideration of mankind's problems of life and destiny, on the basis of scientific understanding, won him wide contemporary recognition. He was elected a member of the three leading learned societies—the American Philosophical Society in 1926, the American Academy of Arts and Sciences in 1934, and the National Academy of Sciences in 1939. A dozen European and South American societies awarded him foreign membership. His alma mater, Indiana University, gave him the honorary degree of Doctor of Laws in 1933, and the Catholic University of Chile made him a Doctor *honoris causa* in 1946.

Dr. Riddle in his last years presented to the American Philosophical Society, in Philadelphia, a collection of his correspondence and other memorabilia, including a typescript copy of the unpublished autobiographical notes upon which this memoir is partly based and a complete list of his publications. His scientific work from 1904 to 1947 may be followed in detail in the successive Year Books of the Carnegie Institution of Washington.

THE AUTHOR is indebted to the late Dr. Benjamin H. Willier for expert comment on much of Riddle's work, especially that on feather patterns.

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KEY TO ABBREVIATIONS

Am. Biol. Teacher = American Biology Teacher
Am. J. Anat. = American Journal of Anatomy
Am. J. Physiol. = American Journal of Physiology
Am. Naturalist = American Naturalist
Anat. Record = Anatomical Record
Biol. Bull. = Biological Bulletin
Cold Spring Harbor Symp. Quant. Biol. = Cold Spring Harbor Symposia on Quantitative Biology
J. Am. Med. Assoc. = Journal of the American Medical Association
J. Biol. Chem. = Journal of Biological Chemistry
J. Exp. Zool. = Journal of Experimental Zoology
J. Nutrition = Journal of Nutrition
J. Pharmacol. Exp. Therap. = Journal of Pharmacology and Experimental Therapeutics
Physiol. Zool. = Physiological Zoology
Proc. Am. Phil. Soc. = Proceedings of the American Philosophical Society
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society for Experimental Biology and Medicine
Sci. Monthly = Scientific Monthly

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