# NATIONAL ACADEMY OF SCIENCES

# CARL RICHARD MOORE

# 1892—1955

A Biographical Memoir by DOROTHY PRICE

Any opinions expressed in this memoir are those of the author(s) and do not necessarily reflect the views of the National Academy of Sciences.

Biographical Memoir

Copyright 1974 National Academy of sciences Washington d.c.



Carekmon

December 5, 1892–October 16, 1955

# BY DOROTHY PRICE

When the distinguished endocrinologist Carl R. Moore died, a document of great importance to a biographer lay in his desk. It was headed "Biographical data prepared for files of National Academy of Sciences," and it was dated August 28, 1948, seven years before his death. Oddly enough, I remember that day and that occasion. I had gone to his office at the end of a particularly hot, muggy, Chicago day and had found him pecking away at an old typewriter in his inimitable fashion with one finger of each hand. When he said that he was writing biographical data for the National Academy of Sciences, I may have been somewhat surprised because he had been a member of the Academy since 1944. In any case, my memory caught and recorded the incident. I was to see the contents of those pages after his death and to recall him vividly as I knew him, the professor under whom I wrote my doctoral thesis in the Department of Zoology of the University of Chicago, the scientist with whom I served as a close collaborator for many years in studies on the physiology of reproduction, the chairman of a department in which I later became his colleague.

What he wrote in 1948 is remarkable in that he painted, quite unknowingly, an extraordinarily revealing picture of his life and scientific career as he saw them. Viewed through his eyes, his career was the proverbial one of the farm boy of limited circumstances who makes good mainly by dint of his own hard work and ambition. It is a typically American story, and in an ingenuous and engaging way he showed his satisfaction and pride that this was *his* story. He had indeed "made good" and could look with understandable pride at his position and accomplishments, his honors and awards.

A biographer who had never known Carl Moore might have been puzzled to find that more than one third of the six pages in his biographical notes of 1948 were devoted to a nostalgic recounting of his experiences on the farm in the Ozark region of Missouri where he was born and to details of his life and early schooling in Springfield. To me, this came as no great surprise. He had often talked at length about his beloved Ozark country background, and the subject was always close to the surface of his mind. But when he wrote these biographical data his thoughts were certainly resting on a past that was illuminated for him by a rosy light. He had recently been granted an honorary degree from Drury College in Springfield, where he had received his B.S. and M.S. degrees. A visit to the scenes of his early years and a reunion with his family had undoubtedly revived old memories. But an additional reason for his preoccupation with his early years seems probable. He had sometimes spoken to me about returning to his Ozark country when he retired, perhaps to a farm near Springfield. In August of 1948, at the age of fifty-five years, he mentioned in his biographical notes that he had nine years before official retirement. He was apparently looking forward as well as backward, and a plan to retire to an ideal country spot near Springfield and its Drury College may well have crystallized in his mind. His life might then have ended where it began, but death anticipated him, and he did not live to retirement.

Carl Moore was born on December 5, 1892, on a farm in Green County, Missouri, twelve miles from the city of Springfield. His father, whose family was originally of Scottish an-

cestry, had been taken from Tennessee to southwest Missouri at the age of ten in a covered wagon drawn by oxen; Moore's mother, whose distant ancestors were English, was born in Missouri just before the Civil War. The farm on which Carl was born was cleared land cut from surrounding forest. Here life was simple, frugal, religious, and relatively primitive, and the boy learned to work hard and to do all the usual farm chores. He also learned to hunt and fish, and fishing remained a favorite outdoor sport and means of relaxation all his life. When he began school, he went to a one-room country school in which the teacher was one of his older sisters.

A new period began for him when he reached the age of nine years and his family removed to Springfield, a town of 20,000 people at that time. In this much less restricted environment, he went through elementary school and high school and entered Drury College. His family had discussed whether he should be "a preacher or a doctor," but the matter must have been settled by the time he registered in college as a premedical student. His tuition was paid largely from money he earned by doing all sorts of odd jobs, such as janitor service, windowwashing, and delivering papers. But it was not all work. He still had time and abundant energy for tennis, horseback riding, hunting, and fishing.

At Drury College, Carl Moore found the teacher who unquestionably shaped the pattern of his future life in scientific research and teaching. Moore should speak for himself on this point just as he did in his biographical data:

"In college, biology in addition to being a rather natural interest from earlier farm experiences, became a favorite subject largely because of the commanding personality of the teacher, Charles Haddon Spurgeon; he was a self-made, jolly, fat man, of large physical stature who inspired youngsters by providing opportunity for work outside the regular curriculum. Being considerable of a critic, his encouragement and com-

mendations were vitalizing. Preparation of slides for histology, serial sectioning of embryos, and many additional activities in the laboratory occupied many all night sessions as well as those on Saturdays and Sundays."

When Moore spoke of Spurgeon's "power over youngsters" he knew whereof he spoke. Spurgeon's example was firmly imprinted on him as a young, eager student. He, too, became just such an inspiring and enthusiastic teacher, and he, too, gave undergraduate students an opportunity to work on projects outside the regular curriculum (often in his own research, with joint publication as an additional bonus). As for dedication to night and weekend work in the laboratory, Moore was a convert, and so were those of us who worked with him. Indeed, it was often necessary for our experiments, but it became a habit and, ultimately, almost a compulsion. It stayed with him in the last years of his life during his failing health, and I would find him in his office on Sunday mornings when he had hardly strength enough to lift his packed briefcase.

At Drury College, extracurricular laboratory work was a joy to the young Carl Moore. It held opportunities for adventure and exploration and a chance to solve the problems he met by some method of his own devising, be it orthodox or unorthodox. I can supplement his own biographical notes with a significant anecdote. When he had difficulty in obtaining good serial sections of embryos because the paraffin blocks crushed, he met his problem in a direct fashion by opening all the windows to let in cold air, putting on overcoat and muffler, and cranking the microtome around to cut again (with better success). There were much simpler and less heroic ways to obtain perfect serial sections, but he did not know them. It is doubtful that Spurgeon knew much about the matter either, but he seems to have given his students free rein to use their own initiative with whatever simple equipment was available and come up with the best results they could.

Moore learned these lessons well. In his own direction of the research of his graduate students, he allowed them free rein for months at a time to let them "find their own feet" (unless they came to him for help and advice). Some floundered hopelessly and dropped out; some completed their research project in a pedestrian way on well-worn paths; but some learned the priceless benefit of being free to develop independence, initiative, and imagination as Moore had learned earlier. They learned, too, to use relatively simple equipment with only the minimum of refined instruments. Money was not wasted on new and showy gadgets-good research did not depend upon such things. Moore was wont to conduct our distinguished guests through our research laboratories, operating rooms, and animal quarters and report to me afterward that he liked to show them what research could come out of a "setup" like ours. And he was right in large measure. An ever-increasing volume of good research was done under relatively primitive conditions; he did not ask for more. In later years, of course, he recognized the obvious advantages of modernization and air conditioning.

We may be sure that there were no special refinements in the Biology Department of Drury College when Moore was studying biology under Spurgeon, learning embryology from Lillie's *Development of the Chick*, and enthusiastically carrying on extracurricular projects. He obtained his B.S. degree in the spring of 1913. His family had no money to send him to medical school, but another opportunity opened. He was offered a position at Drury as an assistant in biology. The position carried a munificent salary of \$100 for the year, and he could work under Spurgeon for an M.S. degree (incidentally, one of the very few ever granted by that institution, as Moore states in 1948). Moore snapped at the chance. But before he began his fifth and final year at Drury, he came to the University of Chicago and registered for summer quarter courses in the

Department of Zoology. Lillie's textbook had caught his interest and piqued his curiosity about the department where the famous embryologist was chairman. Of course, Lillie was not there—he spent every summer at the Marine Biological Laboratory at Woods Hole—but there was much to see and much to learn at the University of Chicago, and it was Moore's first trip away from home.

To obtain his M.S. degree at Drury, which he did in June of 1914, Moore assisted in courses and made what he later termed "an attempt at research" on the origin of the vena cava in bat embryos. He prepared slides of serial sections of embryos, projected the sections on melted beeswax, and by cutting out the projected sections and stacking them he produced models. He had never seen a wax model, but he made some in his own way (undoubtedly with the window open). This research problem might not seem the most interesting one for a young student. For him, it was an exciting foretaste of biological research, and he was thenceforth lost to medicine.

He had applied to some universities for support for graduate study and received offers of fellowships from three. The one he accepted was from the University of Chicago, and in choosing this fellowship he made one of the most important decisions of his life. He would have made a name for himself wherever he had gone, but it is open to doubt whether he would have advanced as rapidly and his name have loomed so large if he had gone elsewhere. Moore came to work with the right man— Frank R. Lillie—at just the right time in the development of Lillie's research program. The Department of Zoology was an ideal environment in which Carl Moore could mature; when he received his Ph.D. degree he was to step into that department as a member just before the beginning of the 1920's, a decade of great and brilliant advances in endocrinology. And Moore was to be in the middle of it all.

However, Moore could not gaze into the crystal ball. When

he went to Woods Hole for the summer session in 1914 and met Frank R. Lillie for the first time, the young man fresh from the Ozark hills was in a state of "uncertainty and trepidation" as he described it. Others, too, had found the dignified, reticent, soft-spoken embryologist overawing. But this first meeting for Carl Moore was a successful one, and he was assigned a doctoral problem in Lillie's large program of studies on the fertilization of the eggs of marine invertebrates.

Lillie became his mentor, and Moore began to learn eagerly the elements of sophisticated scientific research and criticism from one of the best possible teachers. Moore always remained, in a sense, Lillie's protégé, and Moore repaid him with profound admiration, respect, and affection. Fortunately, the young student did not try to emulate too closely the middle-aged man of great distinction who patiently directed him. That would have been disastrous; their backgrounds and personalities were very different. But when Moore later gave the seminars for which Lillie had been famous, "Biology of Sex" and "Physiology of Reproduction," he followed almost exactly not only the lucid organization but much of the subject matter of Lillie's brilliant introductions.

Moore completed his doctoral thesis on fertilization and parthenogenesis in the eggs of a sea urchin in record time and received his Ph.D. degree from the University of Chicago in 1916. He was immediately appointed an associate in the Department of Zoology for the period from 1916 to 1918. He spent half the time in teaching an embryology course designed primarily for premedical students and the remainder in research. In 1918 he became instructor, and in the ensuing years he advanced rapidly, reaching a full professorship in 1928 and the chairmanship of the department in 1934.

In the period from 1919 to 1920 an event of great importance in Carl Moore's life and in his scientific career occurred. A student named Edith Naomi Abernethy caught his attention in

a laboratory section he was teaching. Soon his interest was more than academic, and they were married in July of 1920. He acquired not only an attractive and charming wife, but a hostess who presided with grace and competence on the many occasions when they entertained students and scientific visitors from many places in America (in the broad sense) and abroad. She understood his need to consider his laboratory also a "home," and she shared his love of nature and the outdoors. Their summer home in Michigan was a haven for him and a beloved spot for her. Their honeymoon was spent on a float trip on a river in the Ozarks (where else could it have been?). Two of their three children survived—Harris Mason and Ellen Abernethy.

After publishing his thesis, Moore completed a second paper on the sea urchin, Arbacia, and then turned abruptly to an entirely different line of research in which he was occupied for the rest of his scientific career. The reason was clear, but it requires explanation. Lillie published in 1916 the first of his classic papers on the freemartin, a bovine intersex that resulted from cases of heterosexual twinning when there were anastomoses of blood vessels in the fused fetal membranes. The type of intersexuality and the sterility usually found in freemartins posed intriguing problems. Lillie's observations and his masterful analysis resulted in a theory to explain freemartinism on the basis of masculinization of the female by male hormone produced in the testes of the male co-twin and crossed to the female through the vascular anastomoses. The ovaries were inhibited (antagonized), and the duct systems and glands were masculinized (stimulated). He then proposed that normal sex differentiation in the mammalian fetus might be controlled by bloodborne substances, hormones, secreted by fetal testes and ovaries. However, he cautioned that the theory was only tentative. Nothing was known about the possible effects of female hormone on the male fetus. Fetal gonadectomy-all-important for an under-

standing of normal sex differentiation-had never been accomplished and should be done as a critical test of the theory.

Lillie made "a mild suggestion" (in Moore's words) that Moore try to produce freemartins by experimental means. A mild suggestion was all that was required, and Moore plunged into the problem, or rather into the problems, for his research did not follow any straight path. Thirty-eight years and some one hundred publications later, he still had not produced freemartinism experimentally (nor, indeed, had anyone else). But by then he had developed a theory of his own to explain normal sex differentiation. This proposed that sex hormones from fetal gonads were not controlling normal sex differentiation. The evidence that he presented negated, in his opinion, Lillie's hormonal theory for freemartinism and its extension to normal sex differentiation. However, before Moore was led to this conclusion he made many outstanding contributions in the physiology of reproduction even as he digressed from his original purpose.

Moore began his attempts to subject fetuses to male hormone and produce experimental freemartinism by transplanting testicular tissue onto the membranes of rat and guinea pig fetuses. This failed dismally. Then he transplanted testes into young females in the hope of obtaining freemartins in the litters when these females were ultimately bred. This, too, failed, but he was far from discouraged. He had succeeded in obtaining well-developed testicular grafts in young females. The field of gonad transplantation with its postulates of sex gland antagonism lay open before him.

The Viennese scientist E. Steinach had first reported in 1910 that young spayed female rats and guinea pigs were masculinized when given grafts of testes, and young castrated males were feminized by grafts of ovaries but the hosts *must* be gonadectomized prior to receiving grafts. He therefore pro-

posed and strongly defended, then and later, a concept of sex gland antagonism involving a direct antagonism between testis and ovary.

The question of whether sex gland antagonism really existed was an important one. The validity of such a concept might have a direct bearing on Lillie's theory of freemartinism. Moore promptly sought confirmation or refutation of the concept and soon completely disproved it. He was successful in maintaining testis grafts in young females possessing ovaries and ovarian grafts in young males with testes. In these early experiments of Moore's there was a fortuitous circumstance that undoubtedly favored unusually successful "takes" of the grafts. He routinely exchanged one gonad each between young males and females at the time of grafting, apparently for efficient utilization of animals. Thus the grafts were placed in hosts that had just been hemispayed or hemicastrated. About ten years later, he and I were to propose a theory of balanced control between gonadal hormones and pituitary gonadotropins. The experimental design that he used in 1919 had a sound rationale of which he never dreamed at the time. The grafts that he obtained differed so materially from those described by Steinach that he was led into his next research problems.

Moore's grafts of testes had far better-developed tubules and fewer interstitial cells between them than those of Steinach. The two investigators agreed that spermatozoa were not present in the grafts. Contrary to Steinach, Moore found no evidence for increased hormone secretion and no basis for a contention that testis grafts might effect rejuvenation in senile animals and men.

This fata morgana of warding off all changes of aging in man, or rejuvenating the senile, had appeared again. Testissecreted hormone was the miraculous cure-all. In France, the Russian-French surgeon S. Voronoff was rejuvenating senes-

cent rams by testis grafts. Soon, he reported fantastic results of all kinds in rejuvenation of senescent men with grafts of young human testes and those from monkeys. Voronoff's claims were astounding—and fallacious. Other doctors transplanted testes from sheep, goats, or chimpanzees into aging men, also with reputed success. The craze spread from Europe to the United States. Steinach proposed a new and simpler method in 1920, when he reported rejuvenation of "senile" male rats by vasectomy. He claimed that tying off the excurrent ducts of the testes or removing a segment caused (as in testis grafts) degeneration of tubules and germinal epithelium, compensatory hypertrophy of interstitial cells, and increased male hormone with its rejuvenating powers. A wave of "Steinach operations" spread. Hundreds were done in the United States alone.

In this frenetic period, now all but forgotten, Moore entered the field. He first studied the relationship between degeneration of the germinal epithelium of the testis and the condition of the interstitial cells. Cryptorchidism, the failure of normal descent of the testes into the scrotal sac, was known to be associated with degenerate testis tubules and sterility in man and in other mammals that possess a scrotum. Interstitial cells were known to be increased. Moore and his students produced experimental cryptorchidism in rats and guinea pigs and studied the changes that took place in testes in the abdominal environment and the repair that occurred when such testes were returned to the scrotum.

In Moore's experiments, testicular interstitial tissue was apparently increased, but male hormone production was not increased. More importantly, the germinal epithelium could not remain active nor complete spermatogenesis except in the scrotal environment. Moore's research answered at last the question of the function of the scrotum. He proved conclusively that it acts as a thermoregulator that maintains the testis at a

temperature several degrees lower than that of the abdomen. Only at the cooler temperature can the temperature-sensitive germinal epithelium produce spermatozoa.

This research did far more than answer the academic question of scrotal function; it suggested a method of treatment for the problem of cryptorchidism in man. The medical world listened and remembered. In 1950, the American Urological Association presented him with an award for research on the human male reproductive tract. The citation read, in part: "Dr. Moore is best known to urologists for his researches which elucidated the thermoregulatory function of the scrotum . . . . His experiments were elegant, imaginative and conclusive; they provided a rational basis for the performance of orchidopexy."

While Moore's experiments on cryptorchidism were still in progress, he began studies on vasoligation. With the assistance of his students, he put Steinach's reported effects of vasectomy to critical tests. Again, he disproved Steinach's contentions. Vasectomy, as performed by Moore and his students on five species of laboratory mammals, did not cause general degeneration of germinal epithelium nor increase in interstitial cells (nor, indeed, did it increase male hormone production). Any claims of rejuvenation by means of vasectomy were, therefore, baseless, and the famous "Steinach operation" was worse than useless.

At that time, Moore's scientific career spanned only ten years, but he had made several major contributions. He had disproved the concept of sex gland antagonism and the validity of the "Steinach operation" as a means of rejuvenation; he had discredited the notion of rejuvenation by testis grafts; last but not least, he had proved that the scrotum is a thermoregulator for the testis. These were no mean accomplishments. Moore had already established himself as an authority on several aspects of the biology of the testis and scrotum. His basic findings were of great importance in an understanding of the physiology of

reproduction. In addition, his findings had practical application to medical problems. He was already receiving invitations to address medical meetings and to submit reviews to medical journals and books. This continued all his life; his last publication was in a textbook on urology. He could say what medical practitioners needed to hear in a way they could understand, appreciate, and even enjoy. He was a forceful writer and lecturer and a good showman in the best sense of the word.

In 1927, an extraordinarily fortunate circumstance gave Moore the opportunity to advance his research by new methods. L. C. McGee, a graduate student in F. C. Koch's Department of Physiological Chemistry and Pharmacology in the University of Chicago had just succeeded in obtaining lipid extracts of bull testes which were definitely effective in growth-stimulation of the capon comb and thus contained male hormone. This was a breakthrough, the first major step in the study of testis hormones.

Purification of these extracts depended upon the development of sensitive bioindicator tests for male hormone, and mammalian indicators were particularly desirable. Lillie and Koch arranged an interdepartmental project, and an active research program began. Moore and his team of students and assistants rapidly worked out a number of useful bioindicator methods for testing the male hormone potency of the extracts. Chief among these was the prevention of retrogressive changes in accessory reproductive glands of the rat. Many of the changes that occur in mammalian accessory glands following castration had been known for a long time. However, the findings of Moore and his collaborators gave the first detailed description of the histological, cytological, and secretory changes that resulted from male hormone deprivation and the precise process and rate of restoration of normal structure and function following the administration of testis extract. The accessory glands proved highly sensitive bioindicators. These studies became

classics in the physiology of reproduction and prompted a wide range of other studies. They contributed one of the main bases for an operational definition of an "androgen" and made further important contributions to the recognition that androgens are produced normally not only by testes but also by ovaries and the adrenal cortex.

While experiments on bioindicator tests were still in progress, Moore turned to an old problem. He had earlier disproved the concept of sex gland antagonism (implying sex hormone antagonism). Now he attacked the problem directly by using male hormone extracts and female hormone that was already available. He administered the sex hormones separately or simultaneously to intact and gonadectomized rats. The findings were very difficult to interpret. Some of them suggested sex hormone antagonism, as when the female hormone estrin inhibited the development and function of the testes of young rats. But male hormone also inhibited such testes. Sex hormone antagonism was not the answer: there must be some other explanation. There was! A reciprocal relationship, a negative feedback between the hormones of the gonads and the anterior pituitary gland not only could explain the observations but would fit the results of many other workers into a comprehensive pattern. We quickly tested the idea by using anterior pituitary implants, or extracts, coincidentally with sex hormones. The hypothesis was found valid.

This theory, now known as the Moore–Price negative feedback concept, or Moore–Price "law," or push–pull theory, had wide application in reproductive physiology. It was applicable not only to the relationship between the pituitary and the gonads but also between the pituitary and other endocrine glands. We did not take the next step and link the brain and hypothalamus into the system, nor did we anticipate at that time that our hypothesis would provide the basic principle for "the pill," a contraceptive method preventing ovulation by

the administration of female hormones. However, the late Carl Hartman learned of the theory, recognized just this possibility, and tried unsuccessfully in 1933 to interest clinicians. It was not until 1940 that medical practitioners reported preventing ovulation in women by estrogen, but it was in quite another context. Many more years elapsed before the famous pill emerged.

Moore had finally disproved sex hormone antagonism and substituted the far-reaching concept of a feedback system that controlled gonadal and anterior pituitary function. Lillie was highly enthusiastic. But the freemartin problem was unsolved, and it always remained in the back of Carl Moore's mind as he turned to other research. In the late 1930's this problem came to the fore again, and he tried to cause freemartinism by injecting the male hormone testosterone into pregnant rats. This failed, as had the attempts of others who used the same method. Administration to the rodent of testosterone, a pure steroidal male hormone, did not cause the postulated sex-differentiating effects of fetal testicular hormone.

As confusing and conflicting results accumulated in the literature, Moore sought a different approach and chose the opossum, a marsupial, as an ideal subject for research. In marsupials the young are born in an undeveloped state and maintained in an external pouch where they could be treated with hormones directly (no placental complication here). More importantly, "fetal" gonadectomy could be performed, although it proved to be impossible at early stages and difficult later. However, Moore accomplished it at a stage that he considered young enough to give a critical test of the significance of gonadal hormones in sex differentiation.

The results of his research on opossums convinced Moore that fetal sex hormones play no critical role in sex differentiation. For Lillie's theory he substituted a new one that proposed that the "inherent genetic constitution," male or female, might

400

control male and female sex differentiation; that any or all cells of the male or female body might contribute substances to the bloodstream and, depending on sex constitution, effect male or female sex differentiation. The masculinization of the freemartin could then be explained by humoral substances coming from the whole body of the male co-twin, not just from the testes.

In advancing this theory, Moore undoubtedly believed that he had made a happy compromise. Lillie's humoral theory was retained, but in modified form so that no fetal sex hormones from gonads were involved. Moore's theory did not win general acceptance. His conclusions and interpretations were questioned. However, the results of further research on opossums and on grafts of reproductive tracts of fetal rats confirmed his belief that his theory must be valid, and he published a monograph in 1947. The last important lecture that he gave was in Paris in 1950 at a colloquium on sex differentiation of vertebrates. Here, again, he presented many arguments against the idea that secretions of fetal gonads were important in sex differentiation. He professed himself not convinced that the "proper explanation for the freemartin has yet been suggested." In this he was right; no clear explanation for all the aspects of

freemartinism had been presented then nor has it now. However, the year before Moore's monograph was published, three very important short reports had appeared. L. J. Wells (a former student of Moore's) and A. Jost and A. Raynaud (both in Paris) had succeeded in gonadectomizing fetal rats, rabbits, and mice, respectively. Lillie's critical experiment had at last been done. Fetal testicular hormone was indeed playing a key role in sex differentiation, and much of Lillie's hypothesis was confirmed. Moore found this evidence, and later evidence including results of experiments in my own research project, very difficult to accept. In 1950 he was still unconvinced.

Only a few of all those who heard Moore's lecture in Paris

in 1950 realized how ill he was. Even in 1948 there had been small, ominous warnings that his health was beginning to fail. By 1950 he was barely able to travel to Paris. His health rapidly deteriorated. Between protracted periods of hospitalization he attempted to continue his teaching, research, and administrative duties. He had enormous courage and an unshakable determination to carry on in illness as he had in health. He gave up regretfully some of his committee obligations, but he was unwilling to relinquish any other duties. He struggled to carry what he could no longer carry effectively by summoning sheer courage, determination, and willpower. But Carl Moore would have known no other way. From his Ozark country boyhood through his scientific career he had always solved problems and overcome obstacles as best he could. He bore the grim reality of relentless illness and impending death by negation in the face of hopelessness. The Medal and Certificate of Award of the Endocrine Society was conferred upon him in the spring of 1955, just before the final phase of his illness.

But it is the vigorous Carl Moore of his earlier years who is best remembered—the dedicated and imaginative scientist, the enthusiastic and inspiring teacher, the man of warm and sympathetic character. In his career he valued highly the qualities of fairness, honesty, and just criticism without pettiness. One of his highest compliments was to call a man "a straight shooter." One of his favorite maxims was that "a man must win his spurs" to merit praise and recognition. This was usually applied to a high level of research accomplishment. His students were trained to respect his values. In all, fifteen students obtained the master's degree with him, and thirty-three, the doctor of philosophy. Many of these men and women have "won their spurs" and carried on in his tradition.

Moore was a member of many scientific societies and served as vice president, American Society of Zoologists, 1926; vice president of Section F, American Association for the Advance-

ment of Science, 1943; and president, American Association for the Study of Internal Secretions, 1944. He was active in the National Research Council as a member of the Committee for Research in Problems of Sex, the Committee on Growth, and the Committee on Human Reproduction. He took his share of editorial duties as a member of the editorial boards of the *Biological Bulletin* and of *Physiological Zoology*. He was a trustee of Drury College, Springfield, Missouri, and was awarded an honorary Sc.D. by that school in 1948. Among his distinctions were the Francis Amory Award of the National Academy of Arts and Sciences, 1941; the Award of the American Urological Association, 1950; and the Medal and Certificate of Award, the Endocrine Society, 1955.

# BIBLIOGRAPHY

# KEY TO ABBREVIATIONS

Am. J. Anat. = American Journal of Anatomy
Am. J. Obstet. Gynecol. = American Journal of Obstetrics and Gynecology
Am. J. Physiol. = American Journal of Physiology
Am. Naturalist = American Naturalist
Anat. Record = Anatomical Record
Biol. Bull. = Biological Bulletin
J. Am. Med. Assoc. = Journal of the American Medical Association
J. Clin. Endocrinol. = Journal of Clinical Endocrinology
J. Exp. Zool. = Journal of Experimental Zoology
Physiol. Zool. = Physiological Zoology
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society of Experimental Biology and Medicine

# 1916

On the superposition of fertilization on parthenogenesis. Biol. Bull., 31:137-80.

## 1917

On the capacity for fertilization after the initiation of development. Biol. Bull., 33:258–95.

### 1919

- On the physiological properties of the gonads as controllers of somatic and psychical characteristics. I. The rat. J. Exp. Zool., 28:137-60.
- On the physiological properties of the gonads as controllers of somatic and psychical characteristics. II. Growth of gonadectomized male and female rats. J. Exp. Zool., 28:459-67.
- With F. R. Lillie. A Laboratory Outline and Manual for the Study of Embryology. Chicago, University of Chicago Press. ix + 66 pp.

## 1920

On the production of artificial hermaphrodites in mammals. Science, 52:179-82.

# 1921

- Sex gland transplantation and the modifying effect in rats and guinea pigs. Anat. Record, 20:194. (A)
- On the physiological properties of the gonads as controllers of somatic and physical characteristics. III. Artificial hermaphroditism in rats. J. Exp. Zool., 33:129-71.
- On the physiological properties of the gonads as controllers of somatic and psychical characteristics. IV. Gonad transplantation in the guinea pig. J. Exp. Zool., 33:365-89.

## 1922

On the properties of the gonads as controllers of somatic and psychical characteristics. V. The effects of gonadectomy in the guinea pig on growth, bone lengths, and weight of organs of internal secretion. Biol. Bull., 43:285-312.

#### 1923

- Cryptorchidism experimentally produced. Anat. Record, 24:383. (A)
- On the relationship of the germinal epithelium to the position of the testis. Anat. Record, 25:142. (A)
- With F. R. Lillie. A Laboratory Outline of Embryology with Special Reference to the Chick and Pig. Chicago, University of Chicago Press. ix + 67 pp.
- With R. Oslund. Experimental studies on sheep testes. Anat. Record, 26:343-44. (A)
- With W. J. Quick. A comparison of scrotal and peritoneal temperature. Anat. Record, 26:344. (A)
- With H. D. Chase. Heat application and testicular degeneration. Anat. Record, 26:344. (A)

- The behavior of the germinal epithelium in testis grafts and in experimental cryptorchid testes (rat and guinea pig). Science, 59:41-44.
- With R. Oslund. Experiments on the sheep testis---cryptorchidism, vasectomy and scrotal insulation. Am. J. Physiol., 67:595-607.

- With W. J. Quick. The scrotum as a temperature regulator for the testis. Am. J. Physiol., 68:70–79.
- The behavior of the testis in transplantation, experimental cryptorchidism, vasectomy, scrotal insulation and heat application. Endocrinology, 8:493-508.
- The behavior of the testis under varying conditions and the function of the scrotum: transplantation, cryptorchidism, vasectomy. Minnesota Medicine, 7:753–61.
- On the properties of the gonads as controllers of somatic and psychical characteristics. VI. Testicular reactions in experimental cryptorchidism. Am. J. Anat., 34:269–316.
- With W. J. Quick. On the properties of the gonads as controllers of somatic and psychical characteristics. VII. Vasectomy in the rabbit. Am. J. Anat., 34:317–36.
- On the properties of the gonads as controllers of somatic and psychical characteristics. VIII. Heat application and testicular degeneration; the function of the scrotum. Am. J. Anat., 34:337-58.

## 1925

- Sex determination and sex differentiation in birds and mammals. Am. Naturalist, 59:177-89.
- Testicular displacement and temperature regulation (rat, guineapig). Anat. Record, 31:303. (A)

- The biology of the mammalian testis and scrotum. Quarterly Review of Biology, 1:4–50.
- On the properties of the gonads as controllers of somatic and psychical characteristics. IX. Testis graft reactions in different environments (rat). Am. J. Anat., 37:351-416.
- The activity of displaced testes and its bearing on the problem of the function of the scrotum. Am. J. Physiol., 77: 59-68.
- The relation of the scrotum to germ cell differentiation in gonad grafts in the guinea pig. Am. Naturalist, 60:324-33.
- Scrotal replacement of experimental cryptorchid testes and the recovery of spermatogenetic function (guinea pig). Biol. Bull., 51:112-28.
- On the effects of sex hormones in determining the sex ratio: a criticism of Kovac's paper. Am. J. Obstet. Gynecol., 11:703-05.

## 1927

- A qualitative indicator for the testis hormone. Proc. Soc. Exp. Biol. Med., 24:847–48.
- The motility of spermatozoa as an indicator for the internal secretion of the testis. Anat. Record, 37:119-20. (A)
- The effect of abdominal temperature on spermatozoa of the guinea pig. Anat. Record, 37:120. (A)
- The application of the spermatozoon motility reaction as an indicator for the testis hormone. Anat. Record, 37:120-21. (A)

#### 1928

- On the properties of the gonads as controllers of somatic and psychical characteristics. X. Spermatozoon activity and the testis hormone. J. Exp. Zool., 50:455–94.
- On the properties of the gonads as controllers of somatic and psychical characteristics. XI. Hormone production in the normal testes, cryptorchid testes and non-living testis grafts as indicated by the spermatozoön motility test. Biol. Bull., 55:339– 57.
- With L. C. McGee. On the effects of injecting lipoid extracts of bull testes into castrated guinea pigs. Am. J. Physiol., 87:436–46.

#### 1929

- Studies on the testicle with especial reference to transplantation. Nebraska State Medical Journal, 14:184-87.
- With T. F. Gallagher. On the prevention of castration effects in mammals by testis extract injection. Am. J. Physiol., 89:388–94.
- With T. F. Gallagher and F. C. Koch. The effects of extracts of testis in correcting the castrated condition in the fowl and in the mammal. Endocrinology, 13:367-74.

## 1930

With T. F. Gallagher. Seminal vesicle and prostate function as a testis hormone indicator; the electric ejaculation test. Am. J. Anat., 45:39-69; also in Anat. Record, 44:202 (1929). (A)

With D. Price and T. F. Gallagher. Rat prostate cytology as a

testis-hormone indicator and the prevention of castration changes by testis-extract injections. Am. J. Anat., 45:71–107; also in Anat. Record, 44:203 (1929). (A)

- With W. Hughes and T. F. Gallagher. Rat seminal vesicle cytology as a testis hormone indicator and the prevention of castration changes by testis extract injection. Am. J. Anat., 45:109-35; also in Anat. Record, 44:203 (1929). (A)
- With S. Vatna and T. F. Gallagher. The reaction of the rat vas deferens to castration and to testis-hormone injection. Anat. Record, 45:233. (A)
- The physiologic effects of non-living testis grafts. J. Am. Med. Assoc., 94:1912-15.
- A study of the testicle: effects of increased temperature, transplantation and hormone production. Transactions of the American Association of Genito-Urinary Surgeons, 23:287–96.
- With D. Price. The question of sex hormone antagonism. Proc. Soc. Exp. Biol. Med., 28:38-40.
- With T. F. Gallagher. Threshold relationships of testis hormone indicators in mammals: the rat unit. Journal of Pharmacology and Experimental Therapeutics, 40:341–50.

- A critique of sex hormone antagonism. Proceedings of the 2d International Congress for Sex Research, ed. by A. W. Greenwood, pp. 293-303. London, 1930. London, Oliver & Boyd, Ltd.
- Supplementary observations on mammalian testis activity. I. Vasaefferentia ligation. II. Atypical scrota. Anat. Record, 48:105-19.
- With L. T. Samuels. The action of testis hormone in correcting changes induced in the rat prostate and seminal vesicles by vitamine B deficiency or partial inanition. Am. J. Physiol., 96:278-88.
- The regulation of production and the function of the male sex hormone. J. Am. Med. Assoc., 97:518-22.
- With D. Price. Some effects of fresh pituitary homo-implants and of the gonad stimulating substance from human pregnancy urine on the reproductive tract of the male rat. Am. J. Physiol., 99:197-208.

#### 1932

- With D. Price. Gonad hormone functions, and the reciprocal influence between gonads and hypophysis with its bearing on the problem of sex hormone antagonism. Am. J. Anat., 50:13–67.
- The biology of the testis. In: Sex and Internal Secretions, ed. by E. Allen, pp. 281–371. Baltimore, The Williams & Wilkins Company.

## 1934

With G. F. Simmons, L. J. Wells, M. Zalesky and W. O. Nelson. On the control of reproductive activity in an annual-breeding mammal (*Citellus tridecemlineatus*). Anat. Record, 60:279-89.

## 1935

- Hormones in relation to reproduction. Am. J. Obstet. Gynecol., 29:1-18.
- Testicular biology, scrotal function and the male hormone. New England Journal of Medicine, 212:422–27.
- The testis hormone. In: Glandular Physiology and Therapy, pp. 257-78. Chicago, Am. Medical Assn.; also in J. Am. Med. Assoc., 104:1405-11.
- Hormonal mechanisms in the control of reproductive phenomena. Transactions on the Dynamics of Development, 10:189-203.

#### 1936

- Responses of immature rat testes to gonadotropic agents. Am. J. Anat., 59:63-88.
- With L. J. Wells. Hormonal stimulation of spermatogenesis in the testis of the ground squirrel. Anat. Record, 66:181-200.

#### 1937

With D. Price. Some effects of synthetically prepared male hormone (androsterone) in the rat. Endocrinology, 21:313-29.

Testis hormone secretion and some effects of the hormone in the organism. Cold Spring Harbor Symposia on Quantitative Biology, 5:115-22.

#### 1938

- With J. K. Lamar and N. Beck. Effectiveness of sex hormones administered as skin ointments. Anat. Record, 70:57–58. (A)
- Endocrines and male reproductive behavior. Proceedings of the American Society of Animal Production, 1938:26-33.
- Science at the University of Chicago. Science, 87:278-79.
- With D. Price. Some effects of testosterone and testosterone propionate in the rat. Anat. Record, 71:59–78.
- With J. K. Lamar and N. Beck. Cutaneous absorption of sex hormones. J. Am. Med. Assoc., 111:11-14.

#### 1939

- Biology of the testes. In: Sex and Internal Secretions, 2d ed., ed. byE. Allen, T. H. Danforth and E. A. Doisy, pp. 353-451. Baltimore, Williams & Wilkins Company.
- Modification of sexual development in the opossum by sex hormones. Proc. Soc. Exp. Biol. Med., 40:544-46.
- Gonadotropic substances and male hormone effects in the organism. J. Urol., 42:1251-64.

#### 1940

- Physiology of the testes and therapeutic application of male hormone.
  Bulletin of the New York Academy of Medicine, 16:135–52.
- The biologic background of human reproduction. In: Obstetrics and Gynecology, Vol. 1, ed. by F. L. Adair, pp. 47–72. Philadelphia, Lea and Febiger.
- The testis hormone. In: *The Cyclopaedia of Medicine*, Vol. 14, pp. 932–37. Philadelphia, F. A. Davis Company.
- With D. Bodian. Opossum pouch young as experimental material. Anat. Record, 76:319–27.

## 1941

On the role of sex hormones in sex differentiation in the opossum (Didelphys virginiana). Physiol. Zool., 14:1-47.

Physiology of the testis. J. Am. Med. Assoc., 116:1638-44.

Effects of testosterone propionate on embryonic ducts in the rat.

Archives Internationales de Pharmacodynamie et de Thérapie, 65:365-71.

Embryonic differentiation of opossum prostate following castration, and responses of the juvenile gland to hormones. Anat. Record, 80:315-26.

The influence of hormones on the development of the reproductive system. J. Urol., 45:869–74.

## 1942

- The physiology of the testis and application of male sex hormone. J. Urol., 47:31-44.
- Physiology of the testis. In: Glandular Physiology and Therapy, 2d ed., pp. 233-51. Chicago, Am. Medical Assn.
- With C. F. Morgan. Responses of testis to androgenic treatments. Endocrinology, 30:990–99.
- With D. Price. Differentiation of embryonic reproductive tissues of the rat after transplantation into post-natal hosts. J. Exp. Zool., 90:229-65.

Comparative biology of testicular and ovarian hormones. Biological Symposia, 9:3-10.

#### 1943

- With C. F. Morgan. First response of developing opossum gonads to equine gonadotropic treatment. Endocrinology, 32:17–26.
- Sexual differentiation in the opossum after early gonadectomy. J. Exp. Zool., 94:415–58.

## 1944

- Gonad hormones and sex differentiation. Am. Naturalist, 78:97-130.
- Sex endocrines in development and prepuberal life. J. Clin. Endocrinol., 4:135-41.
- Hormone secretion by experimental cryptorchid testes. Yale Journal of Biology and Medicine, 17:203–16.

## 1945

Prostate gland induction in the female opossum by hormones and the capacity of the gland for development. Am. J. Anat., 76:1– 28.

#### 1946

With E. A. Failor. The role of sex hormones in the origin and development of uterine glands in the opossum. J. Exp. Zool., 102:209-35.

#### 1947

- With H. Wang. Ovarian activity in mammals subsequent to chemical injury of cortex. Physiol. Zool., 20:300–20.
- Embryonic Sex Hormones and Sexual Differentiation. Monograph in: American Lectures in Endocrinology, ed. by W. O. Thompson. Springfield, Charles C Thomas, Publishers. v + 81 pp.
- With D. Price. Reproduction at high altitudes. Anat. Record, 99:574. (A)

### 1948

- Frank Rattray Lillie 1870–1947. Science, 107:33–35; also in Anat. Record, 101:1–4.
- With D. Price. A study at high altitude of reproduction, growth, sexual maturity, and organ weights. J. Exp. Zool., 108:171-216.

#### 1949

Androgens and growth phenomena. Proceedings 1st National Cancer Conference, pp. 67–73.

#### 1950

- Reconsiderations of the influence of genetic factors and steroid hormones in sex differentiation. In: A Symposium on Steroid Hormones, ed. by E. S. Gordon, pp. 393-96. Madison, University of Wisconsin Press.
- The role of fetal endocrine glands in development. J. Clin. Endocrinol., 10:942-85.
- Studies on sex hormones and sexual differentiation in mammals. Archives d'Anatomie Microscopique et de Morphologie Expérimentale, 39:484-94.

## 1951

Experimental studies on the male reproductive system. J. Urol., 65:497-506.

### 1952

Biologic background of male sterility. Fertility and Sterility, 3:453-60.

# 1953

Adrenal cortical secretions in relation to the reproductive system of rats. Journal of Clinical Endocrinology and Metabolism, 13:330-68.

#### 1954

Physiology of the testis and scrotum. In: Urology, ed. by M. Campbell, pp. 123–41. Philadelphia, W. B. Saunders Company.