NATIONAL ACADEMY OF SCIENCES

FRANK RATTRAY LILLIE

1870—1947

A Biographical Memoir by

B. H. WILLIER

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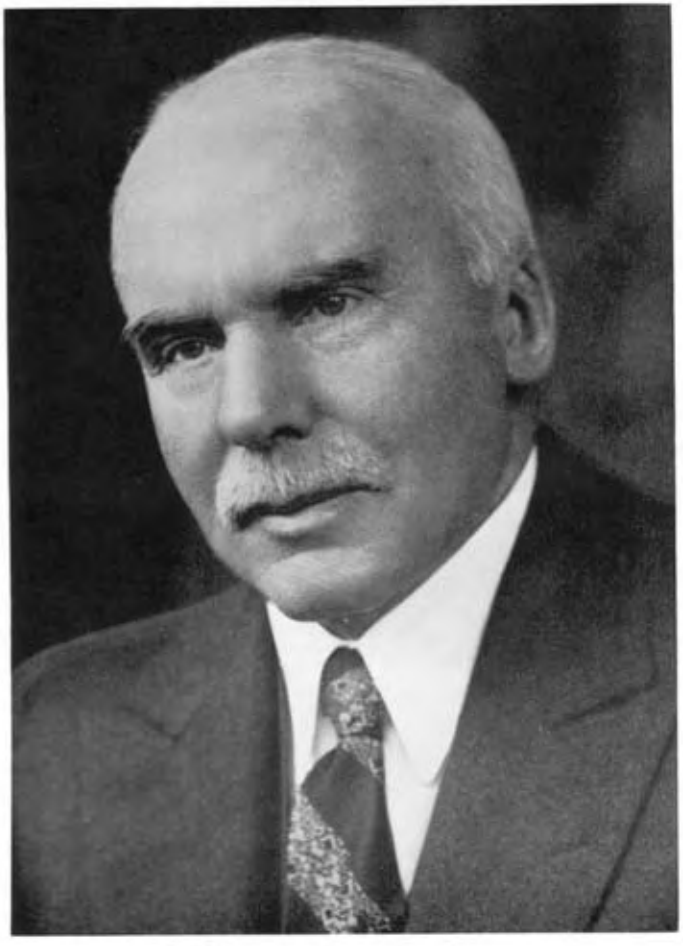

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FRANK RATTRAY LILLIE, whose death occurred in Chicago on November 5, 1947, was a descendant of pioneer families of Scottish and English origin. Three of his grandparents were of Scottish birth and ancestry who emigrated to Canada in the first half of the nineteenth century, his maternal grandmother, Emily Ann Thompson of Halifax, was a descendant of United Empire Loyalists from Salem, Massachusetts, who left there during the American Revolutionary War. Her forebears were of English descent.

Adam Lillie, his paternal grandfather, was a graduate of the University of Glasgow, a Congregational clergyman by profession, and a man of scholarly interests who "read Greek classics in the original" and "at one time was examiner in Sanskrit at the University of Toronto." He was a public-spirited man who served for a while as a missionary to the Indians of Ontario, who addressed public meetings in Toronto, and who wrote a book on the natural resources of Canada entitled *Canada: Physical, Economic, and Social,* published in 1885 by the Maclear Company of Toronto. He founded the "Congregational Academy" in Toronto, which in 1864 was removed to Montreal and there affiliated to McGill University, the first theological college to enjoy this privilege. He was principal of this college until his death in 1869. It was later incorporated in the United Theological Colleges of McGill University. His wife was Elizabeth Waddell of Glasgow, who was characterized as "a very vigorous little Scottish lady."

Thomas Rattray, his maternal grandfather, was a nephew of Thomas Dick, the famous Scottish astronomer. As a young man he settled in Canada; and after accumulating a small fortune in business he became a Congregational minister, serving churches in Concord, Massachusetts, and later in Ontario at St. Catharines. He retired early in life to devote himself in Toronto to theological study and amateur astronomy.

On August 29, 1867, in Concord, Massachusetts, George Waddell Lillie and Emily Ann Rattray were united in marriage. To this couple at their home in Toronto the subject of this biography was born on June 27, 1870, the second in a family of six children, four boys and two girls. The father was an accountant and wholesale druggist, exceedingly upright in character but with no special intellectual tastes. According to notes made by Frank R. Lillie, his mother was devoted to home, church, and friends, and was characterized as "very active, enterprising, and sociable." The home was always a social center.

The foregoing factual sketch may serve to indicate, in part at least, the ancestral background and the environmental setting into which Frank R. Lillie was born and reared. Another factor of probable influence in the shaping of his early interest was the fact that the home of his boyhood was located within walking distance of the center of educational institutions in Toronto. Of his early schooling and development of interest he writes as follows:

"I attended the so-called 'Model School,' a grammar school connected with the Provincial School of Education. I was perhaps an indifferent student, but was especially fascinated by the 'object lessons,' which were scientific talks and demonstrations outside the regular curriculum. I remember one on water, in which we were told that it would expand on freezing, and so at the age of about ten I filled a bottle with water, corked it tightly and left it outside on a cold winter night, and was delighted to find it burst in the morning. Two of our teachers were medical students, and one of them used to

teach us the bones of the body, and I remember also particularly his demonstration on the valves and mechanism of a beef heart.

"The 'Collegiate Institute' which I entered at the age of twelve was one of the municipal high schools, and there my favorite studies were also along scientific lines; although I was beginning to acquire general intellectual interests, I rebelled somewhat against the study of the classics. I spent an extra year in the high school to prepare for the 'Honor Examinations' of the University of Toronto, and entered there at the age of seventeen in 1887, graduating in 1891 with the degree of B.A. At that time the University had a system of group elections and I entered the Natural Science group. After general preparation in the first two years I devoted most of my time to studies in chemistry, geology, and especially in biology. I was very fond of collecting local insects and fossils with the aid of a bosom friend, Alexander J. Hunter, more experienced than I. We kept up these expeditions all through our undergraduate work.

"Many were our discussions on the subject of evolution and its bearing on our strict religious bringing up. He succeeded, as he said, in maintaining a watertight compartment in his brain with one side for science and one side for religion, and later became a minister of the Presbyterian Church, after preliminary graduation in medicine. I was not able to provide such a compartment and science won out against religion, although it had originally been expected that I would follow in my grandfathers' footsteps, but in the Church of England in Canada which my parents had joined."

Although it is clear from the above quotations from the files of the Academy that during the course of his grammar and secondary school education Lillie had a strong leaning toward natural science, it was not until his undergraduate days in the university that he apparently decided to devote his professional life to zoology and not to enter the ministry according to family tradition and expectation. In this decision he was undoubtedly influenced by two distinguished biologists and teachers then on the faculty of the University of

Toronto, Professor R. Ramsay Wright and Professor A. B. Macallum. From the former he acquired an interest in embryology, a special field to which he was to remain devoted throughout life. From the latter professor he appears to have acquired a physiological point of view, a view which later became evident in all of his thinking on embryological theory and research problems. He introduced the expression "physiology of development," thus emphasizing that all of the embryological phenomena have a functional significance.

The die was cast. As a young man of twenty-one in the summer of his graduation, Lillie attended the fourth session of the Marine Biological Laboratory at Woods Hole, Massachusetts. Undoubtedly he learned of the laboratory, which was relatively unknown at that time, through one of his favorite and influential teachers, R. Ramsay Wright, who, it is significant to note, became a member of the Corporation only the previous year (1890) and a trustee the same year that Lillie first went to Woods Hole. Very soon after his arrival that summer Lillie came in contact with Professor C. O. Whitman the first director of the laboratory and one of the early leaders in American zoology. He accompanied Whitman, who at that time was making a study of leeches, on collecting trips to the fresh-water ponds in the vicinity of Woods Hole. On one of these trips they collected the mussel *Unio* bearing eggs and embryos in the gills. In line with the strong interest in cell lineage of the workers at the laboratory in those days, and at the suggestion of Whitman, Lillie began a study of the embryology of *Unio,* in which special attention was directed to tracing the fate of the cleavage cells to future organs of the larva. The investigation was so effective and painstaking that he at once won the praise of all the workers of the laboratory. This led that same summer to his election as a member of the Corporation of the Marine Biological Laboratory and to a fellowship in morphology at Clark University, where Whitman was Professor of Morphology.

During the academic year (1891-1892) he continued his graduate study with Whitman at Clark University. In 1892, Whitman and a

number of other prominent scientists of that institution were lured to the newly founded University of Chicago by its first and very dynamic president, William Rainey Harper. In affectionate admiration and loyalty most of his department and every student went with Whitman. There, two years later (1894), at the age of twenty-four, Lillie received the degree Doctor of Philosophy in zoology *summa cum laude.*

PROFESSOR LILLIE AT THE UNIVERSITY OF CHICAGO

Except for an interval of six years after receiving the doctoral degree, Lillie's professional life was intimately connected with the University of Chicago. For five of these years he was Instructor of Zoology at the University of Michigan (1894-1899) and for one year (1899-1900) Professor of Biology at Vassar College, Poughkeepsie, New York. In the fall of 1900 he returned to the University of Chicago as Assistant Professor of Embryology, remaining there the rest of his life. In 1906, at the age of 36 years, he was appointed Professor of Embryology. Four years later, upon the death of Whitman, Lillie succeeded him as Chairman of the Department of Zoology, a position which he held until 1931, a span of 21 years. From 1931 to 1935 he was Dean of the Division of Biological Sciences. Concurrently he was the Andrew MacLeish Distinguished Service Professor of Embryology, a title in recognition of his distinguished achievement in research as well as of his service to the science of biology at large and to the university. Following his retirement he held this title emeritus until his death.

Lillie early gave evidence of administrative ability and a readiness to assume responsibility. Upon returning to Chicago in the autumn of 1900 as Assistant Professor of Embryology, the day-by-day routine operation of the department soon devolved upon him. In this a flare for administrative astuteness was clearly manifested (likewise apparent in practical operations of the Marine Biological Laboratory at Woods Hole). As Lillie put it, he served as an "understudy of Whitman being groomed, as it were, to be his logical successor."

The Department of Zoology under Whitman was a research department concerned primarily with the advancement of zoological knowledge and with the training of young investigators. To this main objective Whitman adhered quite uncompromisingly with the result that undergraduate teaching was very restricted in scope. However, the university administration had been critical of the department's limited participation in undergraduate education. Consequently, upon assuming the chairmanship in 1910 one of Lillie's first significant acts was to widen the scope and otherwise strengthen the undergradaute program of instruction. In this Lillie was anxious to conform to the policy of the university administration. Nevertheless, he consistently adhered to the Whitman principle of emphasis upon original research and training of graduate students. There was never any intention on his part to de-emphasize the importance of zoological research by himself, his staff, or of the training of graduate students as future investigators. This was of paramount importance to him, as the record in research accomplishment of the department during his administration shows and continues to show after his retirement and death.

As chairman he administered without seeming to do so in simplicity and great dignity. Even in the absence of any declared policy on fundamental principles of departmental administration everyone was aware of them and as a consequence knew his position, responsibility, and opportunity in teaching and research. No one was reprimanded or told what to do. It was a leadership which encouraged both freedom and initiative for the individual, whether staff or student. New appointments or promotions were based primarily on demonstrated ability or promise as investigators; yet effective teaching ability was recognized, appreciated, and respected.

With the growth of the department under Lillie's chairmanship the need for additional research quarters and facilities became increasingly great. Although in 1927 Lillie initiated and energetically set about formulating a plan for a new and modern building for the zoological sciences, he was discouraged by the university ad-

ministration from soliciting adequate funds for the purpose, since funds were more acutely needed for other university developments, particularly in the medical school. He was not to be defeated, however; and the need was met in part when he and Mrs. Lillie decided to finance a research laboratory, which was erected and generously presented to the university in 1936. It was named, significantly, "The Whitman Laboratory of Experimental Zoology" in honor of the first head of the department. This building housed the extensive research programs on the biology of sex initiated and conducted by Lillie and his associates and in addition the research laboratories for ecology, genetics, etc. The Whitman Laboratory stands today as a monument to the research ideals of Whitman and his student, Frank R. Lillie.

As a teacher, Professor Lillie had a far-reaching influence on the quality of performance of the student. Up to about 1916 he taught a one-quarter course in vertebrate embryology (birds and mammals) to medical students and up to about 1924 a two-quarter sequence course in embryology (including principles and theories of development with special reference to maturation and fertilization of the egg, egg organization, cell lineage, formation of the germ layers, and organ formation) to advanced undergraduate majors in zoology and to beginning graduate students. In these courses each lecture was a finished performance and in a way a piece of original synthesis. He always attempted to present a digest of his own generalizations based on his exact knowledge of the original papers in the field of embryology. He had an extraordinary gift for sifting the truly significant data from the published literature and for making generalizations therefrom. Although his lectures were invariably characterized by a masterful plan of organization of factual information and conciseness of statement, they were not always fully effective owing to his soft-spoken and undramatic manner of delivery. It was the example of his austere and studious life that had a long-lasting impression on the student.

Candidates for the doctorate were trained by the seminar method

in which the student was challenged in his report of original literature to exercise judgment in the selection of pertinent data and in making significant interpretations and generalizations. The seminars covered a variety of topics such as Physiology of Development, Problems of Fertilization, and Biology of Sex. In the order named these topics corresponded roughly in time with Lillie's research interests, i.e., to fields in which he has actively engaged in research at the particular time. Although he had made a special contribution in the field covered by each seminar, little or no emphasis was given to his own work. The emphasis was always on the broad aspects of the problems involved. Only outstanding papers were selected for review, particularly those containing new data that led to a new concept or to a modification of an older concept.

It was a deliberate policy of Lillie to assign to his student a research problem for the doctorate which fitted in with his own research program at the time. For example, during the period of intense research on the mechanism of fertilization a number of students were engaged in working and publishing theses on some phases of the problem. Similarly, at a subsequent period when his research interest shifted to biology of sex, the students were working and publishing in the same field. This was a policy to which Lillie vigorously adhered and of which he was justly proud. It promoted a common interest and a closer association between teacher and pupil than would have been otherwise possible. In addition, it assured a comprehensive attack on the problem at large, as the record of publications by his students shows.

In summarizing his influence as a teacher the writer is unable to make a better appraisal than that expressed in the following excerpt from a memorial resolution prepared for the American Society of Zoologists in 1947.

"The student was trained to think by one who directs without seeming to do so, and was attracted first of all to the organization of the seminar and graduate courses in which the results of research, interpretations, and theories were ingeniously knit together around

a central theme. Thus, the alert student was able to see how an apparently insignificant detail was concisely and cleverly woven into a concept with significant implications. The student soon learned to judge and evaluate his own performance in the seminars. The example somehow led him to strive for perfection in organization and clear thinking. The young student when he began research was to a large extent thrown upon his own resources. He found out for himself whether he was fitted to be an independent investigator. Once the problem was suggested and the way of approach briefly sketched, the student knew that results were expected. Only when a preliminary result was obtained did the student report to Dr. Lillie, and even then only when he was prepared to make a possible interpretation." (*Anat. Rec.*, Vol. 100, p. 409.)

In 1931, at the age of sixty-one, he resigned the chairmanship of the Department of Zoology in order to take over an even greater responsibility, the deanship of the Division of Biological Sciences. In recognition of his great value as an exceptionally able and judicious administrator in national affairs (especially as Director of the Marine Biological Laboratory), the university administration invited him to this post one year after the clinical departments of a new medical school were set up on the Midway campus, at which time there existed much dissension and disagreement over organization and management. The clinical departments were envisaged as intimate parts of the Division of Biological Sciences, the largest of the four divisions of the university into which the various departments in art, literature, and natural science were grouped. The task was a difficult one which called for exceptionally able leadership. As Lillie put it, "My special task as dean was to amalgamate the old established preclinical departments with the newly established clinical departments and hospitals into a coherent medical school." Through patience, wisdom, and judicious handling of the situation during his four-year term as dean, he succeeded in his task and brought harmony and understanding into the picture as well as an efficient administrative structure. More than these he succeeded in

uniting the departments of the basic and clinical biological sciences into a closely knit and cooperating group, the like of which too rarely exists in other universities. This working union remains today as a model of what can be accomplished along these lines. This was Lillie's last great achievement in service to the biological sciences within his own university and to other universities as well. In this special achievement he had much personal satisfaction and pride, as his comments to the writer in the summer of 1943 revealed.

BUILDING THE MARINE BIOLOGICAL LABORATORY

As was related above, Lillie first came to Woods Hole in 1891 as a student just graduated from college. From that time until 1946, a period of fifty-five years, he was present at the laboratory every summer. No other person has been associated with the Marine Biological Laboratory for so long a period in its history, or has devoted himself so continuously to its affairs.

In the annual report of the laboratory for the year 1891 he was listed as an "investigator receiving instruction," seemingly very informally, from that inspiring leader, C. O. Whitman. In 1893, the year that the course in embryology was first established in the summer program, he became a member of the staff of instruction and a few years later became head of the Department of Embryology, a position which he retained until 1903.

During the early years of the course at Woods Hole, the study of cell lineage was the foremost topic of interest. This was natural, inasmuch as the majority of embryologists there at that time were actively engaged in investigating the developmental fate of cleavage cells in a variety of eggs of both marine and fresh-water species. In his book on the Marine Biological Laboratory, Lillie aptly referred to the period as "the epoch of cell lineage at Woods Hole." "The work on cell lineage was descriptive and comparative, not experimental, at first; but it was analytic in the best sense of the word."

The validity of the ideas and principles derived from the descriptive and comparative study of cell lineage was soon put to test by

experimental methods which Roux in 1888 and Driesch in 1891 had introduced into the field of cellular embryology. The cleavage cells were isolated by various means and their developmental potencies compared with their normal courses of development. Depending on the species, the isolated blastomeres underwent total or partial development. How could such differences in development be explained? Naturally, explanations were sought in the egg itself, i.e., in its organization upon which the specific behavior of the blastomeres must ultimately depend. The unsegmented egg was subjected to localized defects or to centrifugal force by hand-operated centrifuges. As a result, new theories arose; foremost among them were organ-forming germ regions in the egg (germinal localization) and organ-forming or "formative" substances. There were sceptics, and new ways of attacking the problem were devised and vigorously applied. At the same time the problem of fertilization was being attacked by experimental means. Was the egg activated by the sperm? Could it develop without a sperm? Eggs in appropriate concentration of salt solutions in sea water were apparently activated, and in 1899 Jacques Loeb discovered artificial parthenogenesis.

In the midst of such lively research activity it can be easily imagined how stimulating the course in embryology unquestionably was for the students. They found themselves in an atmosphere saturated with enthusiasm, vigorous discussion, and a variety of opinions, often differing sharply. It was a course in which the highest grade of instruction was furnished by staff members who were thoroughly imbued with the spirit of inquiry and who at the same time were actually engaged in original investigation on embryological problems. Research and instruction went on hand in hand just as Whitman, the director, envisaged it in his first annual report of the Marine Biological Laboratory for the year 1888. Pertinent here are the following lines from Whitman's report:

"Whence the propriety—and, I may say, the necessity—of linking the function of instruction with that of investigation. The advantages of so doing are not by any means confined to one side. Teach-

ing is beneficial to the investigator, and the highest powers of acquisition are never reached where the faculty of imparting is neglected. Teaching is an art twice blest; it blesseth him that gives and him that takes. To limit the work of the laboratory to teaching would be a most serious mistake; and to exclude teaching would shut out the possibilities of the highest development. The combination of the two functions in mutually stimulating relations is a feature of the Laboratory to be strongly recommended."

The ideals so clearly and beautifully expressed above were put to a practical test by Lillie and others connected with the course in embryology. A high degree of perfection was attained and a pattern was set of enduring value, which has served as an ideal model for all courses of instruction in subsequent years at the laboratory.

At Woods Hole, as at Chicago, Lillie early gave every evidence of administrative ability and a readiness to assume responsibility. He apparently began to participate in the day-by-day practical operations of the laboratory soon after he became a member of the staff of instructors in the embryology course. Not long thereafter his ability as an organizer and manager of laboratory affairs was recognized and led in 1900 to his appointment as Assistant Director, a position which he held until 1908. Prior to and during this period of eight years there were recurring struggles and crises over ideals of form of laboratory organization and freedom of self-control versus financial support and security. In 1893, Whitman as director vigorously upheld ideals that are perhaps best epitomized in his own words: "Representative character, devotion to biology at large, independent government,—such as are the essential elements of a strong and progressive organization" (*Atlantic Monthly,* Vol. 71, p. 812). To these ideals of their leader the workers rallied, and as a consequence a revolution took place in the form of government of the laboratory in the summer of 1897. The Board of Trustees was changed from a self-perpetuating (in practice) to an elective body, elected by the members of the Corporation.

Although the laboratory workers had thus won a wider repre-

sentation than ever before and the institution became more thoroughly national in scope, the very difficult and serious problem of securing financial support for maintenance and growth remained unsolved. The need of funds was so desperate and the circumstances so compelling that in 1902 the Corporation and Trustees voted to accept the proposal of the newly established Carnegie Institution of Washington to take possession of the laboratory as their Department of Marine Biology. Once again Whitman was obliged to take a firm stand for his ideals of organization, which to him were superior to any degree of financial security. This he did in a most masterful and persuasive essay entitled "The Impending Crisis in the History of the Marine Biological Laboratory" (*Science,* 1902, Vol. 16, pp. 529-533), one of the most significant documents in the history of the institution. The end result was that the laboratory remained a place where biologists could work in cooperation with one another —completely free from outside control. The fundamental ideals of organization, so vigorously fought for in the midst of much divergence of opinion, have remained unchallenged to this day, a period of over fifty years.

To return to the main thread, it is to be noted that, after success in making these ideals part and parcel of the Marine Biological Laboratory, Whitman gradually withdrew from the laboratory, and upon his resignation in 1908 Lillie was chosen to succeed him as Director. In all of the crises Lillie stood with Whitman. The first grand lessons which he undoubtedly learned from these controversies were those of patience and of how to cope with divergence of opinion. At the same time he impressed his colleagues with his reasonableness and unemotional demeanor. These personal qualities and his experience had prepared him admirably well for effective leadership of the laboratory.

Although the laboratory had thus won independence as a national institution with the center of authority at Woods Hole, the current financial resources were very small indeed. Its greatest asset at the time was the spirit of the workers, their cooperation, inspiration,

and enthusiasm, as well as their faith in the future. This asset was the basis of every claim to a wide financial support. Realizing that funds for maintenance and for further growth were of paramount importance, Lillie in his usual unostentatious manner assumed leadership in searching for avenues of financial support. Certainly as early as 1901 Mr. Charles R. Crane, a brother-in-law of Lillie, began to take an active interest in the affairs and in the support of the Marine Biological Laboratory. That year Mr. Crane was elected a Trustee and, three years later, President of the Board of Trustees and of the Corporation, positions which he continued to hold for twenty years (1904-1924). Throughout that period he contributed substantial amounts each year toward maintenance, as well as real estate property so essential for an expanding and great institution such as Lillie envisaged at Woods Hole.

The laboratory started in 1888 with a single lot (78 x 120 feet) on which the old main building now stands. Like the growth of a crystal by accretion, this single lot formed the nucleus around which land holdings for laboratory purposes were added parcel by parcel over a period of years, very slowly at first, followed by a rapid rate unexcelled in the history of the institution during Lillie's active administration. The accumulation of acreage including harbor frontage was sufficient by 1909 to make plans for the erection of permanent laboratories and wharf facilities so essential to the study of marine biology. It is of interest in this connection to note that Lillie's vision of what the laboratory grounds should ultimately be was not fully realized in his lifetime. In personal conversation with the writer, he envisioned an open plot of landscaped gardens extending westward from the entrance of the present main brick building, replacing thereon the old frame buildings. The purposes which the latter served were to be taken care of by the erection of more permanent buildings elsewhere.

In the accumulation of grounds for immediate laboratory purposes Lillie early recognized that, if the growth of the Marine Biological Laboratory was not to be hampered, land on which the members

and investigators could build summer cottages of their own was a serious need. Available property in the environs of the village was held in large estates at prohibitive prices. Nevertheless, ways were found under the leadership of Lillie to acquire by purchase tracts of land for the purpose. The first of these, the so-called Gansett Tract of 21 acres, was bought in 1916. It was rapidly developed into a community of modest homes for laboratory workers and their families, a development which undoubtedly gave Lillie much satisfaction. Nine years later the Devil's Lane Tract of 105 acres was purchased. In this acquisition it is seen in the quotation below (Lillie, 1944, p. 67) how Lillie at the time had anticipated and envisaged later developments at Woods Hole, especially the founding of the Woods Hole Oceanographic Institution.

"The acquisition of the Devil's Lane Tract in 1925 was also motivated by the consideration that the establishment of institutes representing the physical and chemical sciences might, at some time, be desirable at Woods Hole, not only on account of the already existing close connections of certain aspects of these sciences with biology, but also because the form of organization of the Marine Biological Laboratory constituted a direct appeal to many of their representatives. Such institutions might maintain a relation merely of affiliation with the Marine Biological Laboratory and with one another. They would serve to round out the scientific advantages of Woods Hole and would help to unify the fundamental analytic sciences, not only in their theoretical, but also in their practical or applied aspects. The three sciences of physics, chemistry, and biology are interrelated down as well as up the scale; and the association of representatives during summer months would serve to develop these interrelations—great already in results but of still greater promise. In a practical way, such development would affect medical and industrial research."

As noted above, in 1909 the land accumulations about the old laboratory area had increased to dimensions sufficient to accommodate a new laboratory building, conceived of as permanent in

its construction and modern in its design of research facilities. There was a plan in the background—a growing plan dating from the turn of the century for an expansion and improvement of research facilities. The original working quarters were not only overcrowded but ill-adapted for certain kinds of research, especially of those requiring the use of physiological and biochemical methods. A new laboratory was essential to the Marine Biological Laboratory if it was to win a preeminent place in the broad field of biological research of the nation. The time for action came in December, 1909. In that year Lillie set about with the aid of a committee in the preparation of a well-conceived plan for a building, a first prerequisite for any claim to financial support, as his astute reasoning always demanded in practical affairs. Although the plan was surely convincing, it was "the wonderful spirit that is back of the Woods Hole Biological Laboratory," the spirit of freedom and cooperation that "has been able to accomplish a very great deal with very simple means," which convinced Mr. Charles R. Crane, for at the dedication exercises he said, "For some time back it has seemed to be worthwhile to give this spirit a more substantial body." The "substantial body" took the form of a building, solidly constructed of brick and with concrete floors, complete with equipment in 1913, at a cost of $111,000 and named in honor of its benefactor.

Although the first modern building of the Marine Biological Laboratory, the Crane building was not destined to remain for long the only one of its kind on the grounds. It appears to have been a crucial step in the later development of the institution, as Lillie (*Science,* Vol. 40, p. 230) seems to imply in the following lines taken from his address at the dedication exercises of the Crane laboratory on July 10, 1914.

"The new building stands for a *certain stage reached in the evolution* of this democratic institution; it stands for recognition of a certain degree of demonstrated stability; and for a certain amount of assurance of permanence." (Italics mine.)

Indeed, the Crane laboratory turned out to be a steppingstone in

the further material growth of the Marine Biological Laboratory. "This was in a way our first footing on a permanent basis; the wooden buildings had always been recognized as temporary accommodations" (Lillie, 1925, *Science,* Vol. 62, p. 274). After World War I, workers came to the Marine Biological Laboratory in increasing numbers, and by 1919 the accommodations were inadequate for all who wanted to work at Woods Hole. As Lillie put it, "Another large, modern laboratory had become a necessity." In that year he became the leader in a movement, the ultimate purpose of which was to secure funds for the erection of another building of even greater proportions than the Crane laboratory and for an endowment sufficient for enlarged plant operations. In the "building up" of interest of prospective donors in this movement to provide adequate resources, Lillie used every avenue of approach, by personal and/or official connections with philanthropic foundations or with the National Research Council (cf. Lillie, 1944, pp. 72-75, and Harrison, 1948, in *Biol. Bull.,* Vol. 95, pp. 154-157).

"In this endeavor we received invaluable aid from the National Research Council, which lent our organization its unqualified endorsement and moral support, so sadly needed by a society of impractical professors" (*Science,* 1925, Vol. 62, p. 274).

In all of this he was loyally and ably supported by Dr. G. A. Drew, the Assistant Director, and other members of the Trustees (E. G. Conklin, C. E. McClung, and others), including the President of the Corporation and Trustees, Mr. Crane, who stood ready to assist financially in the great undertaking. In the final analysis it was Lillie's quiet and reasonable way that carried conviction and inspired confidence in all of those who aided him, as well as in the officials of the donor foundations to be.

The "build up " gradually reached a peak toward the end of the year 1921. In January, 1922, the Rockefeller Foundation authorized a gift of a half million dollars toward the construction of a substantial building and endowment for its maintenance, providing that another half million was received from other sources and

that Mr. Crane continue his annual gifts of $20,000. In February of the same year, the Trustees of the Carnegie Corporation approved a gift of $100,000 for endowment purposes only, again with the proviso that the total sum of $1,000,000 must be raised. The next two years must have been anxious ones, for the total amount raised was still short by $400,000 of meeting the conditional grant from the Rockefeller Foundation. In December, 1923, this amount was personally contributed for endowment by Mr. John D. Rockefeller, Jr., through the friendly influence of Mr. Crane. The goal was thus reached and the Marine Biological Laboratory assured of all pledges. Then Mr. Crane through the Friendship Fund, which he established, capitalized his annual gifts so that the laboratory was assured of continued income from securities of the par value of $405,000. Although the funds for endowment exceeded the original estimated needs, there were insufficient funds that could be used for the erection of the building and equipment as planned by the building committee and specified by the architect. Mr. Crane through the Friendship Fund then magnanimously pledged to meet all costs of the building above the half million available for the purpose. This pledge ultimately amounted to over $221,000.

The campaign had been a great success. A total of $1,648,000 had been secured, of which $748,000 was expended for the new building and equipment and $900,000 for endowment. The total resources of the institution then amounted to considerably over $2,000,000. The new building became the main one of the Marine Biological Laboratory in 1925, when it was dedicated and occupied for the first time. With its laboratories equipped for work in all branches of modern biological research and its auditorium, administrative offices, and a library, the building and the annexed Crane wing stand today as an enduring tribute to the spirit of the early workers at the laboratory and especially to Lillie and his associates, who brought this ambitious undertaking to full fruition.

Further developments at Woods Hole were on the way even

while the new laboratory building was under construction. Two needs were immediately pressing, one for special funds to provide for the growth of the library and the other for housing accommodations for the workers. Lillie, through friendship with Dr. Wickliffe Rose, President of the General Education Board, succeeded in gaining his interest in the development, operations, and special needs of the Marine Biological Laboratory. The first result was a gift of $5,000 in 1924 for the purchase of periodicals and books, a need so essential to every investigator. A few years later (1929) the same board made a gift of $200,000 for endowment of the library. The growth of the library received such a strong impetus from these gifts that within a decade the available stacks became inadequate for the books and periodicals. Accordingly, by 1942 a new five-story extension, solely for library purposes, was built at a cost of $110,000, provided by the Rockefeller Foundation. The original library with its extension has storage accommodations for over 180,000 volumes and ample provisions for study tables among the books, as well as a spacious reading room, a cataloguing room, and an office for the librarian. Thus, during the lifetime of Dr. Lillie, the library became, to use his words of an earlier date, "a library that we aim to make the best possible source of reference in the field" (*Science,* 1925, Vol. 62, p. 272). Indeed, it attained the distinction of being one of the leading biological libraries in the nation, if not in the world. In this development Lillie took a personal interest, as he revealed in conversation with the writer on several occasions. However, he was always very alert and responsive to any suggestions for improving the library for the investigator.

The second need, a long-felt one, that of safe and comfortable living quarters for the workers, had become a pressing one, so much so that, to use Lillie's phrase, it "again threatened the natural growth of the Laboratory." Apparently a little more persuasion was required to secure funds for such purposes than was the case in obtaining funds for the growth of the library. Nevertheless, after "the extent and nature of the need" had been thoroughly

studied and presented, the officers of the General Education Board were convinced and in 1926, only one year after the main brick building was completed, appropriated $250,000 for the erection of a dormitory and an apartment house, both to be of fireproof construction and in appointments and furnishings modern but modest. Both of these buildings were completed and occupied by many investigators and/or their families for the first time in the summer session of 1927.

Finally, in order to give an over-all picture of the magnitude of the achievement, it is of interest to compare the material assets of the Marine Biological Laboratory at the beginning and at the end of the period of Lillie's active administration. In 1900, when he became Assistant Director, the total assets including land, buildings, and endowment amounted to an estimated value of only $35,000. In 1941, the year before he retired as President of the Trustees and Corporation, the assets of the laboratory had been increased by a hundredfold. In his chapter on "The Material Growth of the Marine Biological Laboratory," Lillie (1944) summarizes as follows:

"The land, buildings, library, and equipment represented expenditures of about $1,980,000 up to 1941. The major and minor endowment funds amount to about $1,125,000; the value of the interests of the Laboratory in a biological supply house and a public garage on a very conservative capitalization of income amounts to at least $280,000. The total resources are thus $3,385,000, and there is no indebtedness.

"The gifts of the great benefactors tend to overshadow the contributions of others to the material growth of the Laboratory; but, if we reckon with the spirit of the givers, the merits are equal. The reports of the first ten years contain long lists of persons who, by gifts, testified to their faith in the infant and set it firmly on its feet; and, since that time, there have always been many others ready with gifts of money or service to aid in general or special needs. These, by faith and sacrifice, created the confidence on which the material development was based. The annual reports record

numerous instances, but it is the unrecorded spirit on which the past has depended and on which the future hangs."

On this achievement his contemporary, Professor Edwin G. Conklin, comments as follows:

"Many members of the Staff, Trustees, Corporation, and many devoted friends and organizations contributed to this great growth, but the leader in gaining the confidence and support of financiers and of great foundations was Frank R. Lillie." (*Biol. Bull.*, 1948, Vol. 95, p. 162.)

The accomplishments of Lillie at the Marine Biological Laboratory cannot be measured alone in terms of material things, like land, buildings, and endowment. There were other achievements of equal importance but less tangible and less easily appraised. He was gifted with scientific insight, administrative ability, and business sense, a rare combination in any one man. As an active investigator for a long period, both at Chicago and at Woods Hole, he had a real appreciation and understanding of the ways of the investigator; moreover, he grasped quickly the newer trends in biological research and was thus prepared to encourage and support any new developments in the field at large. New ways and techniques of attacking old and new problems always fascinated him. Such qualities in a director must have been of great value in setting a high standard of research accomplishment of the workers of the laboratory.

In his own way he was the leader in the perpetuation and interpretation of the initial ideals of his predecessor, C. O. Whitman. Indeed, the wisdom of Whitman's stand for independence and the democratic ideal of scientific organization was proved to be sound and effective—even to a few sceptics who in early days had favored a benevolent despotism. In this accomplishment, his successor as Director, Dr. M. H. Jacobs, commented on the occasion of Lillie's sixtieth birthday as follows:

"To Dr. Lillie more than anyone else the Laboratory owes its freedom from certain features of our American system of institu-

tional management which are particularly irritating to scientists. To have preserved during the critical period of its enormous material expansion the atmosphere of freedom and informality which characterized its earlier days and to have kept alive the spirit of hearty cooperation which makes it possible for the group of scientists who compose the Corporation and the Board of Trustees to manage the affairs of their own institution without a cumbersome administrative machinery, without the services of efficiency experts, and with an almost unbelievable absence of friction of any sort, is a contribution of outstanding importance, not merely to the Marine Biological Laboratory but to Science and Education generally."

On the same occasion just referred to above, the late Professor Edmund B. Wilson characterized admirably well the qualities of Lillie that enabled him to accomplish so much, in the following excerpt from his address:

"As I look back on Lillie's long service I am impressed especially with two of its aspects. One is the unassuming and seemingly easy manner in which that service was rendered. The tasks that he had to perform were often delicate and difficult, but he had a way of making them look easy; and he carried them through with a good sense and absence of fuss and fury that are beyond all praise.

"The second noteworthy thing in the record is the manner in which he kept a steady hand on the helm without creating jealousy or hard feeling among the crew. In this respect his record seems to me especially noteworthy. Differences of opinion, of course, there have been; but I am not able to recall a single instance in which those differences led to personal animosities. I am afraid that he sometimes had a hard team to drive. He succeeded because he did not try to drive. The effectiveness of his leadership lay in the tactful and fraternal way in which he maintained and carried forward our traditional policy of cooperation and democracy in scientific administration."

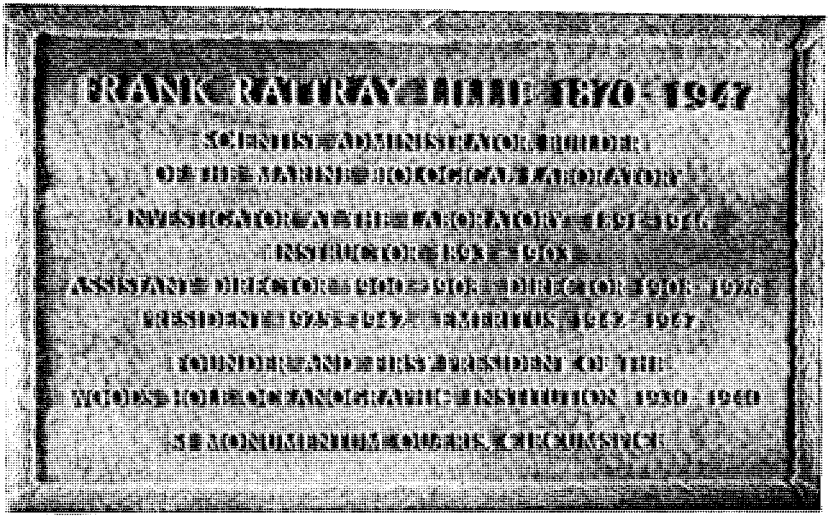
In still another direction Lillie showed an extraordinary ability,

i.e., in the management of financial affairs. Early in the campaign for financial support on a large scale, he apparently gave careful consideration to the handling of the anticipated endowment funds. The problem was an unusual one, for, unlike the trustees of most educational institutions, "The trustees of the Laboratory, as scientific men, were not accustomed to problems of investment and were naturally afraid of such responsibilities" (Lillie, 1944, p. 83). In collaboration with the Treasurer of the Corporation and the President of the Rockefeller Foundation, a plan was worked out whereby the anticipated endowment was to be held in trust for the benefit of the Marine Biological Laboratory by a competent trust company. The plan was endorsed in principle by the trustees in 1921, and in January, 1924, a deed of trust was duly signed by appropriate officials.

This deed of trust is a significant document in the history of the laboratory, for it not only solved the problem of handling large endowment funds but also provided legal safeguards for insuring permanently the use of income for the promotion of biological research as well as for guaranteeing high standards of performance in biological research.

Lillie's understanding of the way of the investor is well illustrated in the purchase in 1919 of a controlling interest in the General Biological Supply House of Chicago. The motivation behind this decision was apparently twofold in nature: (1) to keep the business of the Supply Department of the Marine Biological Laboratory under manageable proportions in order to preserve its primary purpose of service to investigators and instruction; and (2) as a rewarding investment. With respect to the latter he seemed to have had foresight rather than intuition. He knew personally and had confidence in the management of the General Biological Supply House. Its policies of service to biologists together with the assured growth of the biological sciences in American institutions undoubtedly led Lillie to believe that this supply house gave every promise of vigorous growth. It actually fulfilled all expectations as a supply house and for many years has yielded the Marine Biological Lab-

oratory dividends which annually exceed in value the original capital investment. Each year as he reported the income from this investment, those who knew him best could detect the incipient smile of satisfaction. It is no wonder that, following an interview with a reporter, one of Chicago's leading daily newspapers referred to him as the "banker zoologist!"



FOUNDING OF THE WOODS HOLE OCEANOGRAPHIC INSTITUTION

Although it is not known just when the notion of an institution for the study of the sea itself first formed in the mind of Lillie, in all probability he was toying with the idea long before anybody else knew about it. However, it is clear that as early as 1925 he envisaged the establishment of other institutes in affiliation with the Marine Biological Laboratory and in serving "to round out the scientific advantages of Woods Hole." In any event, by that year—the year that the new main building of the Marine Biological Laboratory was dedicated and first occupied—the conferences and correspondence between Lillie and Wickliffe Rose, then President of the General Education Board, had turned to the subject of

oceanography and in particular to the need of an oceanographic institution on the eastern coast of the United States. In the latter part of the same year, a definite plan of procedure had crystallized for the realization of the project. The strategy decided upon was to obtain the backing of the National Academy of Sciences; for its prestige, as Lillie understood better than anyone else, would have a far greater influence than would the recommendations of individuals in winning support for the enterprise. But before the matter was brought to the Academy, nearly two years were spent in preparing the way, or, as Lillie records it, "after considerable waiting for conditions to become favorable." During that period arousal of interest in oceanography became widespread throughout the nation.

The time for action came in the spring of 1927. At the annual meeting of the Academy that year, during the presidency of A. A. Michelson, the following motion was presented and unanimously approved:

"That the President of the Academy be requested to appoint a Committee on Oceanography from the Sections of the Academy concerned to consider the share of the United States of America in a world-wide program of Oceanographic Research and report to the Academy."

As his contemporary academician, Professor Ross G. Harrison (*Biol. Bull.,* Vol. 95, p. 155), later expressed it, "Lillie's presentation of the case must have been persuasive to secure such prompt action for the committee was appointed immediately with Lillie as chairman, . . ."

Soon thereafter the Committee was at work. No time was lost, for a little over a year later, in the summer of 1928, thanks to a liberal appropriation of $75,000 from the General Education Board, a series of conferences was held at the Marine Biological Laboratory. As Lillie expresses it in his book on Woods Hole, "The purpose of the conferences was to acquire information concerning the present status and problems of oceanographic research, especially

in Europe and America, and to lay the ground for a study of the best ways in which to supplement American agencies" (p. 178). Participants in the conferences included American and European representatives familiar with the manifold problems of the sea. In this manner the problems became clearly defined to the Committee. Dr. Henry Bigelow was then invited to make investigations and to assemble all findings in a report for the Committee. In November, 1929, a little over a year after the conferences were held, a preliminary though extensive report was submitted to the Academy and approved by it. For purposes of this account the report contained one recommendation of special significance, to wit, "the establishment of a well-equipped oceanographic institution in a central location on the Atlantic Coast." Although no specific mention was made in the report of the exact location, by the end of the summer of 1929 Woods Hole had already been definitely selected as the site "on account of its geographical advantages and scientific good will and co-operation assured there" (Lillie, 1944, p. 180).

Even prior to the formal endorsement of the Committee's report by the Academy, the way was cleared for the realization of the plan. Apparently Lillie had thought out and anticipated subsequent events, for in 1927 he had an informal understanding with Wickliffe Rose, whose retirement from the presidency of the General Education Board was imminent, regarding the tentative cost of establishing and maintaining an oceanographic institution (the figure arrived at was three million dollars, which was exactly the sum finally provided). Dr. Rose, who had shown from the beginning a deep interest in the sea, was determined that his final project would not default upon his retirement. He, therefore, made arrangements for the transfer of further considerations of the project to the Rockefeller Foundation. It is interesting to note that, just five days before the report was approved by the Academy, the trustees of the Rockefeller Foundation had granted authority to its executive committee "to aid in the construction and support

of the proposed central Atlantic Oceanographic Institute," contingent, however, upon favorable action of the members of the Academy. This interlocking of action was apparently not without foresight and of much significance in the outcome of the plan.

The Academy gave its approval on November 18, 1929. Just two days later, an agreement was reached in conference with the officials of the Rockefeller Foundation to the effect that the site for the proposed institution should be provided by the Marine Biological Laboratory and that the members of the Academy Committee on Oceanography should constitute "a nucleus of a Board of Trustees" to which other men of prominence and action should be added. The latter was essential for purposes of incorporation and of insuring a responsible body for the conduct of the affairs of the institution.

Early in January of the next year, the Act of Incorporation of the Woods Hole Oceanographic Institution in the Commonwealth of Massachusetts was duly approved. Whereupon—just nine days later—the first meeting of the Board of Trustees was held in New York, with the avowed purpose of organizing that body. Nevertheless, Dr. Max Mason was there by invitation and on that occasion informed those assembled that the Executive Committee of the Rockefeller Foundation was prepared "to consider a formal request from the Woods Hole Oceanographic Institution for funds sufficient to establish the institution on a permanent working basis, with the understanding that the necessary land would be taken care of by others" (Lillie, 1944, p. 182). The formal request must have been forwarded with dispatch and the action on it by the Executive Committee of the Foundation likewise rapid, for on February 13, 1930, a grant of $2,500,000 was appropriated. Of this sum, $1,000,000 was designated for building and other construction, boats, and equipment, $1,000,000 for endowment, and $500,000 for current expenses over a period of ten years. In 1935 annual grants of the last were replaced by a permanent endowment of $1,000,000, a gift from the Rockefeller Foundation. In the end Lillie was correct in

his estimate of the funds required to set up and run an oceanographic institution such as he visualized at the beginning. There was one unforeseen snag in the plan, namely, the legal right of the Marine Biological Laboratory to transfer the site of land to the Oceanographic Institution without adequate remuneration. This was soon resolved (October, 1930), however, by a gift of $27,000 from the Carnegie Corporation to cover the appraised value of the site.

Events moved very quickly after the financial support of the institution was assured. Architects had to be engaged to draw up detailed blueprints for the laboratory building with pump house, dock, float, and sea wall, contracts let on a competitive basis, etc. Nevertheless, by July, 1930, construction had commenced. The building was completed and opened for occupancy on June 15, 1931. In addition, a seagoing vessel, essential to the effective operation of the institution, had to be designed, competitive bids secured, and the vessel built. The result was a motor ketch, the *Atlantis,* which was docked at the wharf of the institution at 6 o'clock on Monday evening, August 31, 1931. To any outside observer the speed of accomplishment in the great enterprise—a period of just six years between the initial steps (1925) and its full realization (1931) —was an achievement worthy of acclaim.

Lillie naturally became the first President of the Corporation, serving from the time of the organization meeting in 1930 until his retirement in 1939. During that period of nine years, he watched over the growth of the Institution from infancy to maturity with wise counsel, not only in its physical plant but in its research accomplishment in various branches of oceanography. In addition, he saw with much satisfaction the fulfillment of two other intentions of the founders: (1) the provision for the training of beginning investigators and of facilities for visiting independent investigators met with marked success, so much so that in 1939 over one hundred workers, representing twenty-nine different institutions, five of them located in foreign countries, were accommodated; and (2) the original plan of service as a center of coordination of

oceanographic research of governmental agencies and private institutions, especially on the Atlantic Coast, met a real need. Cooperative arrangements in oceanic research with various governmental agencies, universities, and laboratories quickly materialized and continue today on an even wider scale.

As a consequence of collaborative thought and planning, the Woods Hole Oceanographic Institution became during Lillie's lifetime one of the leading institutions of its kind in the world. In recognition of his part in this great accomplishment, the National Academy of Sciences awarded to him in 1940 the Agassiz Medal. In the citation, Professor E. G. Conklin said in part:

"In all this labor of awakening interest in oceanography, in securing large endowment, in building and equipping the station and in organizing its main lines of research, Dr. Lillie took the leading part ably seconded by Dr. Bigelow.

"This is the leading privately endowed oceanographic institution in the world. Already it has drawn to itself many of the leading oceanographers of the world. Its research ship, the *Atlantis,* has sailed more than 150,000 miles on research voyages; more than 240 research papers and monographs have been published from the institution since its foundation. The National Academy of Sciences may well be proud of the fact that it took so important a part in sponsoring this notable institution, without any cost to itself.

"For his important researches and his wise leadership in marine biology, for his enduring contributions to the science of oceanography in the founding and endowing of the Woods Hole Oceanographic Institution, for his modest but effective leadership in causing this country to assume its share in a world-wide program of oceanographic research, the committee on the Murray Fund presents to you, Mr. President, for the eighteenth award of the Agassiz Medal, Frank Rattray Lillie." (*Science,* Vol. 91, p. 414.)

Conceived before others dreamed of it, founded in 1929, realized in 1931, the Woods Hole Oceanographic Institution stands and

functions today as Lillie would have it, a companion to the Marine Biological Laboratory "in the study of the ocean and its abounding life from different viewpoints and different methods." To him it was "in some sense an offspring of the Marine Biological Laboratory."

SCIENTIFIC WORK—AN APPRAISAL

Simultaneously with all of his exacting duties and responsibilities as administrator in various capacities, Lillie not only maintained a keen and abiding interest in the progress of research in biology and cognate fields but was engaged in original research himself. An examination of the record and his bibliography at the end of this memoir will show a continuous devotion to research from the summer of 1891, when he began work on cell lineage with Whitman for the doctorate degree, to 1944, a period of over fifty years. In addition, he directed the research of many graduate students on problems related to his at the time. As Lillie put it in 1943, "At all times during my investigations I have had graduate students who were carrying on related pieces of investigation, so that what I could personally do was multiplied many times."

As noted above, his first work was on cell lineage, a subject of common interest and wide exploration by embryologists at the time. In his first main scientific contribution, "The Embryology of the Unionidae. A Study in Cell-Lineage," Lillie at once gained recognition as an able embryologist among his contemporaries. Although this paper was his doctoral thesis, it showed patience and accuracy in observation, a gift for critical and logical analysis, as well as a comprehensive insight into and an understanding of the problems of the organization of the egg and its cell lineage in various invertebrates. To him as well as to others of the period this was a field which seemed to hold promise of revealing some of the mysteries of how a new and complex individual lies determined in the substance of the egg. A special feature of his study of cell lineage of *Unio* was the discovery, as Lillie related it in 1943, "that the behavior of the individual cells was adaptive and

that varying sizes, rates and divisions of cells were directly related to the subsequent events." To him development at any particular time and locus is always a special feature directly related to functional need. Lillie's main point of view regarding cell lineage is epitomized in his lecture on "Adaptation in Cleavage," delivered in the summer of 1898 at the Marine Biological Laboratory. Whereas other investigators on the subject laid special emphasis on the resemblances between the cleavage pattern of eggs of even widely separated forms (gastropods, lamellibranchs, annelids, and turbellarians), Lillie in contrast emphasized another aspect of cell lineage, to wit, "the special features of cleavage in each species, which are, I believe, as definitely adapted to the needs of the future larva as is the latter to the actual condition of its environment." To him "the peculiarities of cleavage in *Unio* are but a reflection of the structure of the glochidium, the organization of which controls and moulds the nascent material." Herein lies a partial insight into his philosophy of embryonic development.

Thus, by reflection on the meaning of the orderly and specific behavior of the individual cells during normal cleavage in the formation of specific parts of the glochidium larva of *Unio,* he was well prepared to explore the nature of organization of the egg itself. Somehow the material basis for cleavage pattern must reside in the protoplasmic substance of the unsegmented egg. From studies of his contemporaries at Woods Hole, Lillie correctly discerned that the egg of the tubiculous polychaete annelid, *Chaetopterus pergamentaceus,* was far better adapted than that of *Unio* for the purpose. As Jacques Loeb queried in January, 1901, could the unfertilized egg of this marine annelid, when treated with KCl in proper concentration, differentiate without any visible external signs of cleavage? That very summer Lillie set about and completed a thorough study of the effects of a short exposure of eggs to abnormal concentrations of potassium in sea water. In words of his 1902 paper, "The results have proved to be unexpectedly interesting." Indeed, unsegmented eggs, both fertilized and unfertilized,

underwent well-defined phases of differentiation in the absence of either cell division or nuclear division. A ciliated unsegmented body formed which in shape, structural features, and motility simulated closely a normal trochophore of a corresponding age. Referring to this discovery in 1943 (personal notes to the Academy), Lillie says, "Among these [his research accomplishments] I would cite as especially significant the study of differentiation without cleavage, that is to say, the kind and amount of development that might take place without any cell division, though accompanied by an immense increase of nuclear substance. This was theoretically important at the time, when the subject of cell division played such a role in theories of development." This discovery was at the time and still is regarded as a classic on the subject of the degree to which the events of differentiation and growth (cell multiplication) are independent of each other.

Surely the capacity to differentiate in basic outline certain specific morphological features of a trochophore is present in the unsegmented egg of *Chaetopterus*. After a cytological examination of the minutiae of the changing disposition of visibly different substances in the egg cytoplasm during the course of maturation and fertilization and of their differential spatial distribution during cleavage and subsequent stages, Lillie studied the effect on egg development of the redistribution of visible substances by centrifugation. If the unfertilized egg at the period of the first maturation spindle was centrifuged at a moderate speed (1,500-2,000 r. per minute) and then fertilized, the egg underwent normal cleavage, even though such visible materials as endoplasmic spherules and microsomes had been abnormally distributed by the centrifuging. Clearly the polar organization of the egg was unmodified. Thus the conclusion could be drawn that polarity is dependent "on some configuration or heterogeneous physical or chemical properties of the ground substance established early in the history of the egg and which is not essentially disturbed by centrifuging. In other words, that there is a definite architecture in the ground

substance, which is the basis of the localization pattern in normal development" (Lillie, 1909, p. 60). To him the so-called "organ-forming substances" or "formative stuffs," terms then in common use, are "really germinal areas probably including a variety of substances, and distinguished only by their localization and by the useful but superficial character of color" (Lillie, 1906, p. 257). He was puzzled, however, by the strictly determinate distribution of the visible components in normal development; but he considered them as not without meaning, since the surviving eggs exhibited a distinct tendency toward abnormalities.

In sum, through a combination of exact observation and experiment Lillie was led to formulate the stimulating concept that polarity (and likewise bilaterality after fertilization) is a property of the ultramicroscopic structure of the egg, i.e., a "firmly organized ground substance" within which "the flowing movements are simply granule movements." Although this concept had a marked influence on embryological research and thought for a score of years, more recent studies have indicated that the ultrastructural basis of egg polarity is probably localized in the egg cortex (ectoplasm), the chief component that was relatively unaffected by centrifugation in Lillie's experiments.

The dynamic changes that take place in the egg protoplasm of *Chaetopterus,* especially at fertilization, immediately led to a study of the mechanism of fertilization of the egg, a subject that was to engage Lillie and his students for a period of over ten years (1910-1921). Altogether he published 17 original contributions, excluding several papers published as theses for the doctorate by his students. The work was brought together in 1919 in the form of a small, lucidly written book entitled *Problems of Fertilization* and again in 1924 (in collaboration with his devoted and distinguished student, the late E. E. Just) in a revised and expanded version.

His approach to the problems of fertilization was both biological and physiochemical, methods of analysis that are, as he emphasized in 1919, in "inevitable conflict" and which "will long continue

to exist, but there is an ultimate reconciliation, if not in sight, at least in prospect on logical grounds." Such a combination of methods of inquiry served him well, for it led to a far deeper understanding of the processes of fertilization than would have been possible had he adopted a single mode of approach. In this manner he became recognized as an outstanding investigator in the field.

The marshaling of the myriads of facts throughout the course of painstaking and careful investigations and observations on fertilization in echinoderms and nereid worms led Lillie to become increasingly emphatic in support of the conclusion that the process of fertilization involves a series of precisely timed, irreversible, and species specific reactions between the egg and sperm that culminate in egg activation. As an end product of reflection on the meaning of the substantial body of accumulated facts, the so-called Fertilizin Theory was formulated in order to picture the mechanism of fertilization and thereby point "the way to a more inclusive theory that shall comprise all the main aspects of fertilization" (Lillie, 1919, p. 267). A notable feature of the theory (cautiously regarded by Lillie as only serving "as a working hypothesis") is that it applied for the first time the then current immunological concept and terminology to the interaction of specific substance borne by the egg and sperm. These substances were conceived as linked and reacting with one another in the manner of lock and key combinations. This interpretation, though adversely criticized by several of his contemporaries at the time (see Just, 1930, *Protoplasma,* Vol. 10, pp. 300-342) has turned out to be essentially sound in its conception as later investigations on the subject have indicated (see A. Tyler, 1948, *Physiol. Rev.,* Vol. 28, pp. 180-219). Thus, in bringing the various facts and theory in due relation to one another Lillie was able to point out where solid ground lies and to indicate by implication in what direction further studies may go. To him, sound speculation was the primary stimulus for future research and advancement of knowledge and understanding.

The foregoing account gives in chronological order the chief

accomplishments in research on cellular embryology at the Marine Biological Laboratory. Paralleling these accomplishments is a record of sustained research at the University of Chicago. Almost from the beginning of his academic career at Chicago, Lillie had a deep interest in the chick embryo as a favorable object for the analysis of embryological problems and argued that "the best introduction to the problems opened up by the study of embryology is a careful first hand study of some one species." To this end he had prepared an extensive series of serial sections of the chick embryo at various stages, the study of which provided the basis for many of the original contributions made in his book *The Development of the Chick* (1908). In his words, "This book is a plain account of the never-failing resource of the embryologist, the chick." Indeed, on the broad and secure foundations of developmental morphology as laid down for the first time in this work rests the great structure which has since been built in the field of experimental embryology of the chick.

Prior to the date of publication of *The Development of the Chick*, Lillie initiated a program of experimental studies on the chick embryo—the original object of which at the outset[1] was an attack on the problem of correlative differentiation (i.e., "the influence of intraorganic environment in development"). To him "any process of self-differentiation (Roux) of a structure might be analyzable into correlative differentiation of its parts" (1903, p. 3). His personal contribution to this subject was limited to one major paper, in which

[1] It should be noted here that the very first experiments Lillie ever performed on chick embryos were made primarily to ascertain whether or not the wing bud or other parts might regenerate after extirpation. Although in 1904 he succeeded in showing that "the embryo of the chick possesses no greater power of regeneration than the adult," it is clear from views on correlative development expressed in his 1903 paper that the removal of one part surely must have an influence on other parts in embryogenesis. Indeed, within a span of five years his student, M. L. Shorey, published a significant paper showing that extirpation of the forelimb rudiment has a profound effect on the development of nerve centers.

the conclusion was reached that the whole process of amnion formation is set astray by "a slight injury to a part of the early rudiment" of the amnion, thus comprising "an extremely good example of correlative differentiation." This work stands today as perhaps the most significant contribution to our understanding of the forces responsible for the elevation of the amniotic folds. Although Lillie was very much aware of the importance of correlations in the developmental process, his major role was played in bringing this realization home to his students.

With these modest beginnings, the stage was set for an era of intensive analysis of the mechanisms of development of the chick embryo and its parts. Gaining momentum somewhat slowly during the second decade of this century, the experimental method has since risen in marked rapidity to its present high peak of perfection in the solution of the dynamics of chick development. Techniques of isolation, of operation, and of grafting to the chick embryo through a small window in the shell—techniques that once seemed difficult or impossible—have been devised and successfully applied. Chick embryology thus entered in its most advanced phase, that of experimental analysis. In all of this progress almost up to 1947 Lillie was a witness who took great satisfaction and pride in the accomplishments of his students and his "scientific grandchildren," and were he with us today he would be pleased that the goal remains as always the establishment of new concepts or the modification of old ones as revealed by analytical studies on the chick embryo.

As the book *The Development of the Chick* was nearing completion, Lillie was already reflecting on problems of sexual differentiation, an area in which he was within a decade to make an original contribution of distinction. On December 28, 1906, in an address before the American Society of Naturalists on "The Biological Significance and Control of Sex" (*Science,* Vol. 25, pp. 372-376), he argued that in the zygote (fertilized egg) "we must find the primary cause of sexual differentiation" and seek an answer to the question as to "how the differentiated conditions are subse-

quently produced." To him the old concept of a sexually indifferent stage in the life history "is as necessary and fundamental today as it ever appeared to be, and that we cannot depart from it without involving ourselves in absolutely hopeless theoretical difficulties." Thus, at that time, Lillie clearly and accurately envisaged that the determining conditions established in the egg at fertilization act so as to direct the course of development of characters in either the male or female direction, and further that sex characters arise, as do other characters, in a certain order of succession in embryogenesis. Apparently at or about that time, as subsequent events imply, Lillie had a hunch which had to be tested by observation or experiment.

Thus, by prolonged and assiduous thinking Lillie was prepared for chance events that came about several years later on the family farm northwest of Chicago near the village of Wheeling, Illinois. Here in his prized herd of purebred cattle his attention was apparently first drawn to the "freemartin," a term popularly applied from ancient times by experienced cattle breeders to a barren female which is born co-twin to a normal bull calf. Such an unconformable case in twinning naturally posed the question as to whether the sterility of the female was a causal consequence of its association with a male partner during uterine life. Was this an experiment in nature that would test Lillie's hunch that mechanisms in the control of differentiation of sex can be analyzed?

In searching for an answer to this question twins *in utero* had to be obtained. Fortunately this was made easy and feasible by the not-too-distant location of the university to the Union Stockyards, where large numbers of cattle are slaughtered daily. By alerting a foreman of an abattoir of Swift and Company to be on the lookout for pregnant uteri with twins (the younger the better) and with the loyal help of the departmental collector, the twin-bearing uterus ideally with both ovaries attached was rushed to Lillie's laboratory table for immediate examination by him.

So far as can be ascertained from the record, Lillie began in the

autumn of 1914, a systematic examination of fetal twins *in utero*. By February 25, 1916, a total of 41 cases of bovine twins had been studied with such exactness of observation that no critically important detail was overlooked. The observations were pregnant with meaning and decisive, and furnished the basis for his announcement in *Science* two months later of "The Theory of the Freemartin." Thus, within a period of a little over one year he had worked out the distinctive and peculiar conditions essential for the formation of a sterile freemartin. The definitive paper based on a grand total of 55 pairs of fetal twins was published in July, 1917.

First of all it was essential to establish beyond a shadow of doubt that the sterile freemartin is a zygotic female and not a male co-zygotic with its mate. Almost all authors up to 1916 had interpreted the freemartin as a male co-zygotic with its mate, an inference based primarily on the male-like internal reproductive organs (i.e., testes in the groin and a gubernaculum of the male type) of the freemartin. Likewise, as Lillie admits, he adopted at the beginning of the investigation the "working hypothesis" that the freemartin and its partner are identical twins (i.e., of monozygotic origin) of the male sex. On such an assumption the freemartin must be interpreted as a modified male; and, as Lillie stated, "the explanation of the modification must be found in the twinning process itself, i.e., in the division of the single zygote that *ex hyp.* formed the two twins" (1917, p. 375). With this aim in mind he studied fetal twins *in utero* pair by pair, always on a lookout for data of key significance. Only after collecting data from 27 cases of fetal twins was he fully and finally convinced that the freemartin and its co-twin did not arise from a single zygote but from two distinct zygotes. Apparently, Lillie had not anticipated during the early stages of the investigation that sex hormones could possibly play a role in causing the transformation of the female by its male partner. Only later (1917, p. 384) did he argue that "it is impossible to suppose that the association of two males *in utero* should cause the

transformation of one of them into a freemartin in a certain definite proportion of cases."

The decisive answer to the question of the zygotic origin of the freemartin and its mate came from the embryological evidence. As Lillie admits, it was a great surprise to discover that nearly all bovine twins *in utero* were monochorial, a condition usually regarded as evidence of monozygotic origin. That the twins, whether of the same or opposite sex, really arose from two zygotes, however, was established by showing that for each embryo a *corpus luteum* was present—one in each ovary—and further that, although originally independent and in opposite horns of the uterus, the chorionic vesicles of the two embryos, owing to their great tendency for elongation, met in the connecting body of the uterus and fused secondarily therein. No longer was there any doubt in Lillie's mind that the freemartin and its mate arose from separate zygotes. Could the freemartin possibly be a zygotic female? Lillie argued that the freemartin is female, since it is impossible to conceive how the association of two males could cause the sex transformation of one of them. Moreover, the external genitalia and mammary glands of the freemartin are almost invariably of the female type. Finally, as Lillie (1917, p. 384) put it, "The assumption that the freemartin is a male leads to an absolutely incomprehensible sex-ratio, while the interpretation that it is female comes nearer fulfilling the expected sex-ratio." Although basically sound, these arguments left unexplained the mode of origin of the male-like nature of the internal organs of reproduction in the freemartin.

Treating the freemartin as a zygotic female, the question naturally arose as to the nature of the conditions essential for its transformation in the male direction. In a nutshell, Lillie discovered that when the fetal membrances of male and female embryos are intimately fused and the allantoic blood vessels (especially the arteries) of the twins are united so as to permit a constant interchange of blood, the female is modified in the male direction. The transformation may be so complete that the female develops testes and male sex ducts

instead of ovaries and female sex ducts. However, if no blood vascular connection develops, even though the fetal membranes are fused, both male and female partners are normal in sex development. To Lillie such a condition served as "a veritable *experimentum crucis,*" as indeed it was. Fetal vascular connection became *sine qua non* for the sex transformation of the female. As Lillie put it in 1916, "This is unquestionably to be interpreted as a case of hormone action." Moreover, since the effect was limited to the formation of male sex characters in the female, he regarded the effective agent in the process as a male sex hormone.

Coequal in importance with the discovery of embryonic sex hormones was his original contribution to the understanding of the mode of their action in altering sex development. With keen insight into the problem he established that the vascular connections of the fetal membranes usually became suitable for the intermingling of blood of the two embryos during the morphological indifferent period of sex development or at about the time of onset of sex differentiation. At these critical stages the rudiment for each male structure that develops in the freemartin is already present in the female. On this point Lillie (1917, p. 419) stated, "In the case of the freemartin we do not find that the male hormones cause the development of any structure which is not represented embryologically in the normal female; the hormones act in this case by inhibition or stimulation of normal embryonic rudiments." Therein a new concept had its inception—one that foreshadows our modern conceptions that the role of sex hormones is to actuate the expression of latent differences in reactivity preexisting among the tissue components of a reproductive system that is basically bisexual in its embryonic organization. Thus, at the time when nothing was known about the subject, Lillie succeeded in indicating where solid ground lies and in what direction further effort might usefully be exerted.

The unraveling of how "nature performed a crucial experiment" (as Lillie phrased it) on the question of the role of sex hormones

in the embryonic differentiation of sex characters is a model of scientific analysis. In it serendipity, rigorous logic, penetrating insight, and creative interpretation as well as perfection of exploration are displayed. Although the minutiae of detail comprised an essential part of the analysis, the goal to him, as in all of his major investigations, was to discover new principles. Verily, Lillie succeeded in laying down the principle that "the course of embryonic sex-differentiation is largely determined by sex-hormones circulating in the blood" (1917, p. 415). After nearly four decades of research by many workers on the role of sex hormones, this remains today a general truth of wide application in understanding the embryonic development of sex characters—one on which others have been founded.

The uncovering of a new phenomenon introduced biologists to the problem of the nature, origin, and action of sex hormones at a time when almost nothing was known about the subject. The effect was immediate and widespread. It started many researches, in this country and abroad, initially designed to test the hormonal theory of the freemartin by experimental means. During the decades that have passed since the original observations and theory were reported, the hormonal interpretation of the freemartin condition has not infrequently been criticized. Quite possibly the theory is inadequate, but the surest way to prove it inadequate is by demonstrating that the evidence on which it is based is unreliable. No one has questioned the evidence; in fact, confirming evidence was furnished independently and almost simultaneously by Keller and Tandler (1916) in Austria and still later by several others.

That the purely hormonal interpretation of the freemartin condition, however, may need to be qualified and enlarged is suggested by recent studies showing that the modification of sex development is not the only change that takes place. The accompanying changes are of a more subtle nature. The majority of dizygotic twins in cattle, whether of like or unlike sex, have identical red-cell antigens owing to an exchange of circulating blood cells between them dur-

ing fetal life (Owen and others); and, furthermore, contrary to theoretical expectation, skin homografts reciprocally interchanged between them are to a high degree mutually acceptable (Billingham, Medawar, and others). Accordingly, the freemartin as well as its male mate contains a mixture of genetically female and male blood cells (red-cell precursors of different antigenic types)—a situation which clearly corresponds to the anomalous conformity in antigenic properties of the skin of the twins. Whether a causal connection exists between such changes and the one-way change in sex development remains an open question. On the basis of current research, the possibility must also be recognized that organ-specific molecules other than hormones are present in the circulation of an embryo, and consequently in the intermingling of blood of twin embryos of unlike sex they may have a far-reaching effect in modifying the sex development of the freemartin. To explain the one-way effect is today as puzzling as it was to Lillie in 1917. As Lillie would have it, the theory of the freemartin only serves to uncover new phenomena that still require explanation in endless succession.

In all of his research, as is clearly evident in the printed record, Lillie regarded the experimental approach in the laboratory as adding a finishing touch to those "experiments" that are always taking place in nature. To him both methods of approach to a problem are necessary and complementary. In the production of the freemartin condition nature had seemingly provided almost as wide a range of requirements of a "good experiment" as might be imagined by an ingenious investigator in designing experimental procedures. Yet, Lillie clearly recognized the desirability of testing and extending by experimental artifice the role of sex hormones in controlling the differentiation of sex characters of the vertebrates at all stages in the life history. To this end he immediately initiated among his colleagues and students a broad and intensive program of research on the isolation and purification of sex hormones and on their role in regulating the expression of sex characters. For his own phase of the program he wisely chose for exploration the

Brown Leghorn fowl, a breed which displays in a most striking manner a sexual dimorphism in plumage color and pattern. In collaboration with his research associates (especially Dr. Mary Juhn and Dr. Hsi Wang), clues as to the nature of the processes concerned in the action of hormones (estrogens and thyroxin) in the production of color pattern of the feather were disclosed.

The feather papilla or germ during regeneration proved to be a morphogenetic system in miniature, displayed such characteristic features as bilateral organization, inductor-like action, and gradients in reaction time and threshold to hormones. Indeed, as an embryonic system, the growing feather papilla provides a well-ordered functional background in which color and pattern on the finished feather become elaborated in a precise and orderly manner in response to the action of female sex hormones or thyroxin. Furthermore, feather papillae in different positions on the body vary not only in morphogenetic pattern but also in the kind of color reaction given to hormones. These discoveries remain today as the most significant contributions yet made to the intricate and complex problem of the nature of the interconnections between morphogenesis, hormones, and events in color differentiation of the feather. In elucidating these and similar problems Lillie was active almost to the end and finished his scientific career on the theme of the underlying mechanisms of plumage color design in birds—as he envisaged, keys that would unlock the investigator's way to a better understanding of the natural beauty of birds.

RELATIONS TO LEARNED ORGANIZATIONS

It is not surprising, from the foregoing account, that this phase of Lillie's life and activities should be intimately bound up with his tangible accomplishments as an investigator and his reputation as an able administrator. Recognition and honors were bestowed upon him by numerous scientific societies, academies, and universities. He was elected a member of the National Academy of Sciences in 1915 and of the American Philosophical Society in the following

year; likewise, a fellow of the American Academy of Arts and Sciences, a correspondent of the Academy of Natural Sciences of Philadelphia, an honorary fellow of the Royal Society of Edinburgh, and a foreign member of the London Zoological Society; also, a member of the Société Belge de Biologie, Société de Biologie(Paris), and Société Royale des Sciences Médicales et Naturelles de Bruxelles. The honorary degree of Sc.D. was conferred upon him by his alma mater, the University of Toronto (1920), and by both Yale (1932) and Harvard (1938) Universities, and the LL.D. by Johns Hopkins University (1942).

As regards his formal relations to scientific societies, he served as President of the Central Branch of the American Society of Zoologists (1905-1908), of the American Society of Naturalists (1915), and of the National Academy of Sciences (1935-1939). In an autobiographical memorandum in the Academy files Lillie says, "Among the offices I have held in various scientific societies those that I value most were the Presidency of the National Academy of Sciences (1935-1939) and the Chairmanship of the National Research Council (1935-1936) held simultaneously with the first year as President of the National Academy of Sciences. I resigned the Chairmanship of the Council because I felt that it was not good policy to continue to subordinate the Council so much to the Academy; a single year was sufficient to restore the constitutional relations which had become seriously strained previously."

The year after Lillie was elected to the Academy, the National Research Council was established. During his first years as academician there is no indication of any active participation in Academy-Council affairs. As one of his contemporaries remarked, "His modesty and observing character must naturally have led him to assume a waiting attitude until he became familiar with its procedures." The tide turned, however, in 1919, when he was chosen by the American Society of Zoologists as one of its first representatives in the newly organized Division of Biology and Agriculture of the Council, an assignment he held for four years. At once he

was made a member of the executive committee of the Division under the chairmanship of C. E. McClung. In this position an opportune moment had come to Lillie for action on what was foremost in his mind at the time, namely, ways and means of securing funds for building a greater Marine Biological Laboratory at Woods Hole. He presented his case before the Division in 1919, whereupon he was appointed chairman of a committee to investigate the need for a broader basis of support of the laboratory, an institution of distinction in its nationwide scope. The report of his committee endorsing the program of the Marine Biological Laboratory was formally and heartily approved by the executive committee of the Division and the executive board of the Council. Then, as Lillie relates it in his book on the history of the laboratory, through Vernon Kellogg, permanent secretary of the Council and also a member of the Executive Committee of the Rockefeller Foundation, "access" to the officers, including the President, who had been a colleague of Lillie at the University of Chicago, was "facilitated." These interconnections led, early in 1922, to a conditional grant from the Foundation; and by the end of the next year all of the specified conditions were met, so that the laboratory could go ahead with its plans for the erection of a new building and for an extension of the library—also with the assurance of a modest but permanent endowment. In the bringing this ambitious enterprise to fruition Lillie looked upon the National Research Council as playing the role of lending its "unqualified endorsement and moral support." All in all, "Lillie's account of these events sounds somewhat naive in view of all the invective that has been hurled at interlocking directorates, but it evidences a wholly honest spirit without fear of criticism for taking advantage of personal and official connections in such a good cause" (Harrison, 1948, *Biol. Bull.,* Vol. 95, p. 155).

In 1922 Lillie, after a period of one year as Vice Chairman, was chosen Chairman of the Division of Biology and Agriculture, a position he held for one year. Prior to taking on these positions he

had been working hand-in-hand with his predecessor, C. E. McClung, on a plan to provide the biologists of America and of the world with adequate abstracting service. To this end the Union of Biological Societies was organized in 1922, and by 1926 had assumed responsibility for the publication of *Biological Abstracts.*

Another project brought to fruition during his chairmanship was the establishment in 1923 of the National Research Council Fellowships in the Biological Sciences through an initial grant of $325,000 from the Rockefeller Foundation. As chairman of the fellowship board from its inception until 1931, he played a leading role in determining its policies and procedures. In 1937 the fellowships in the physical and biological sciences were merged into the National Research Council Fellowships in the Natural Sciences. On this joint board Lillie served for two years. In commenting upon the development and success of the fellowship program as a whole, Lillie, in 1936 (*Science,* Vol. 84, p. 279) said, "To have led the way in the development of this essential addition to the older plans for advanced training has been a much prized privilege of the National Research Council."

In 1921 a Committee for Research in Problems of Sex was set up in the Division of Medical Sciences of the National Research Council with Lillie as one of the appointed members. Owing to his pioneer discoveries on the relation of sex hormones to sex differentiation and to his wide knowledge of the biology of sex, he was able to contribute materially to the work of this committee for a period of sixteen years. During this period scores of investigators were assisted by financial aid (administered by the committee from grants provided by the Rockefeller Foundation), by suggestion, recommendation, and other forms of advice. As a way of celebrating the completion of a decade of service to investigators, the committee sponsored the preparation and publication of *Sex and Internal Secretions* (1932), a volume that testifies eminently to the diligent labors and wise decisions of the committee members. In fact, within a period of five years of its issuance the new discoveries in the field

had expanded so rapidly that a thoroughly revised new edition (published in 1939) was demanded by acclaim of literally hundreds of workers in the field. To be of service with others in furthering research by others in all branches of biology was one of Lillie's outstanding characteristics.

As a consequence of his demonstrated administrative skill, personal qualities, and readiness to assume responsibility both at the University of Chicago and at Woods Hole, he was unanimously elected simultaneously President of the National Academy and Chairman of the National Research Council in 1935 at the age of 65. As Ross G. Harrison commented, "This unusual action was taken in order to relieve a situation that had arisen in the relations between the Academy and the Council, which harked back to the appointment of the Science Advisory Board several years before and which required a man of Lillie's poise and experience to adjust" (the "situation" referred to here is more fully related by Harrison in *Biol. Bull.,* Vol. 95, p. 156). He went about his task with unruffled determination and assurance; and, by the end of the first year of office in this dual post, Lillie had succeeded in bringing about smooth working conditions between the two organizations, so much so in fact that he relinquished the chairmanship of the Council. In referring to these matters in 1939 Lillie wrote, ". . . my strong conviction [is] that the Academy and Council are one and indivisible," a conviction that, as he further noted, "gained strength" during the ensuing three years of his term as President of the Academy. Among the many expressions of gratitude for his accomplishments as an elder statesman, one stands out in written record, to wit, "I always thought that through the force of his integrity and high esteem in the scientific world he was able to create in the minds of a number of other opposing members of the Academy a better understanding of the place of the Council in the Academy's structure."

As the thirteenth President of the Academy, through both formal and informal relations, he acquired a working familiarity with most if not all of the specific activities and accomplishments of

innumerable committees of the Academy and Council, which, as he noted, "are described, if not verified, in the grave and gray pages of reports." Save for the first year of his presidency no unusual happenings are recorded. Nevertheless, real advances were made in several directions. First among them was a strengthening of the Academy and Council relations to the agencies of the Federal Government. As his presidential address in 1939 shows, Lillie took a special interest and care in promoting these relations in strict conformity to the obligations of the charter to the Academy. A second event of interest was the birth in 1938 of the Pilgrim Trust Lectureship, which resulted from a "fertile union of ideas" among officers of the Royal Society of London and the Academy. The idea behind the establishment of the lectureship was that of providing mutual hospitality through an exchange of lecturers between the two organizations. Supported by a grant from the Pilgrim Trust, six distinguished scientists were exchanged between 1938 and 1946. Regretfully, this arrangement is now in abeyance for lack of funds. Still another accomplishment of note was the establishment through a grant from the Rockefeller Foundation of the Central Purposes Fund, a fund that was urgently needed for the financing of conferences on projects of national and international interest.

In closing this section of the memoir dealing with Lillie's role in the Academy-Council affairs it seems fitting and appropriate to set forth the following pertinent excerpts from the tribute that President A. N. Richards paid to him at the autumn meeting of the Academy in 1947.

"Concerning Dr. Lillie's term as President of the Academy I shall say little because I know little. I know that through his influence, certain confusions which had developed in the relations between the Academy and the Government were resolved, that during the first year of his term he accepted the additional burden of the Chairmanship of the National Research Council, becoming the only person in the history of the Academy and Council who had simultaneously held these two positions. I know that it was during his admin-

istration that the Pilgrim Trust Lectureships were created which resulted in a most distinguished exchange of lecturers between this country and Great Britain. I believe that during his term a unification was achieved in the program of fellowships in the natural sciences financed by grants from the Rockefeller Foundation. It was also during his term, as what I have said before has indicated, that the final steps which led to the establishment of the Oceanographic Institution in which the Academy had such a vital interest were taken.

"It was not my good fortune to have had more than a casual acquaintance with Dr. Lillie. I remember vividly his appearance as he presided at an Annual Meeting of the Academy in 1939. He gave an unforgettable impression of dignity, keen intelligence and precision of thought.

"With what I admit is insufficient knowledge, I link his perfectionistic attitude of mind with that which I knew to be possessed by my old teacher, R. H. Chittenden of Yale—an attitude of distaste amounting to scorn of anything less than the greatest possible thoroughness, and accuracy of thought and nicety of performance.

"To many who did not come into close touch with him, myself included, he gave an impression of austerity and reserve. I have it, however, from one who worked with him and under him for many years in the Woods Hole laboratory that in this respect appearance was deceptive. No questions which concerned his science or the Institution which he loved were too trivial to take to him; but in the consideration which he gave to them the unimportant dropped out of sight, only the essentials were left. In helping to revise the opinions of others, as he was often called upon to do, there was never a hint of humiliating criticism or reproach. He must have possessed a deep understanding and a very subtle sense of humor; otherwise he could never, in the administrative difficulties which he faced, have brought harmony into being; he must have known well how to 'suffer fools gladly.'

"The record which he established, of long and able guidance of

a great university department, of that of a chief builder of two great research institutions, of distinguished leadership for a period of the National Academy and the Research Council, and of the affectionate devotion of a host of pupils and colleagues, I think you will agree, marks a career which could well be called incomparable." [2]

[2] The readers of this memoir will find some supplementary facets in the personal and professional life of Frank R. Lillie in the following selected references:

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KEY TO ABBREVIATIONS

Amer. J. Physiol. = American Journal of Physiology
Amer. Mus. J. = Journal of the American Museum of Natural History
Amer. Nat. = American Naturalist
Anat. Rec. = Anatomical Record
Biol. Bull. = Biological Bulletin
Biol. Rev. = Biological Reviews
J. Exp. Zool. = Journal of Experimental Zoology
J. Morph. = Journal of Morphology
J. Proc. Add. Assn. Amer. Univ. = Journal of Proceedings and Addresses of the Association of American Universities
Physiol. Zool. = Physiological Zoology
Pop. Sci. = Popular Science
Proc. Inst. Admin. Off. Higher Inst. = Proceedings of the Institute for Administrative Officers of Higher Institutions
Proc. Nat. Acad. Sci. = Proceedings of the National Academy of Sciences
Yearb. Amer. Philos. Soc. = Yearbook of the American Philosophical Society
Zool. Bul. = Zoological Bulletin

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