

NATIONAL ACADEMY OF SCIENCES

DAVID HILT TENNENT

*1873—1941*

---

*A Biographical Memoir by*  
MARY S. GARDINER

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

*Biographical Memoir*

COPYRIGHT 1951  
NATIONAL ACADEMY OF SCIENCES  
WASHINGTON D.C.



*D. H. Tennant*

## DAVID HILT TENNENT

1873-1941

BY MARY S. GARDINER

David Hilt Tennent was born on May 28, 1873, in Janesville, Wisconsin, one of the younger children in the large family of Thomas and Mary Hilt Tennent. He was of Irish and American ancestry. His father, as a young man of 19, left the town of Newtonhamilton in County Armagh, Ireland, to come to the United States to make his living. In so doing he followed the example of other members of the Tennent family, devout Presbyterian ministers, who had emigrated to the United States a hundred years earlier. William Tennent created and to a great extent built with his own hands the little theological school—Log College at the Forks of Neshaminy near the Pennsylvania-New Jersey border—in which a notable group of young men including his own sons Gilbert, William and John, were trained as Presbyterian ministers and from which they went forth to preach the Gospel. Although not in direct line of descent from them, David Tennent was always proud of the part these representatives of his family had played in the spread of religion and in the development of scholarship in America.

David Tennent's father, Thomas, settled in Cambridge, Massachusetts, married and had two children. Later he went to Janesville, Wisconsin, where he married a second time. His second wife was Mary Hilt, a Philadelphian by birth, and David was the fourth of her six children. Thomas Tennent was a contractor and the family life was simple, even austere. Each child had his share of tasks that had to be satisfactorily done and each had to earn what he could for his own needs, with little left for the satisfaction of even small desires. The Tennent children had a rigorous and not particularly happy childhood, and they early learned to accept the responsibilities of life and to meet them punctiliously and uncomplainingly.

David Tennent received his early education in the public schools of Janesville. He was, as far back as he could remember, fired by anything scientific and when he reached high

school age set up a chemistry laboratory in an empty room of his parents' house where he carried out experiments of his own devising. He longed to study medicine, but any hopes that he might have had of realizing that dream vanished when, in 1893, his father died from the effects of an accident, a year after David's graduation from high school. That year he had spent as a clerk in a drugstore, earning what money he could and devoting all his free time to the study of pharmacy, the best substitute he could find for the medical training he so much wanted. Self-taught from the United States Dispensary except for the practical knowledge he picked up in the drugstore and the bits of information and advice that the general practitioner of Janesville gave him, he prepared himself for the Wisconsin State Examination in Pharmacy and passed with the best record ever previously made.

But before he had practiced long as a licensed pharmacist a way was opened for him to enter a liberal arts college and in 1895, helped by one of his older sisters, he enrolled in Olivet College, Olivet, Michigan. During the five years of his undergraduate studies there he acted as assistant in science; the first year in chemistry and the last four in biology, studying and working under the direction of Hubert Lyman Clark, who later became Curator of Marine Invertebrates in the Museum of Comparative Zoology at Harvard. Professor Clark had but recently taken his doctor's degree at Johns Hopkins University and, when his pupil and assistant had received his B.S. degree with honors at Olivet in 1900, Clark encouraged him to enter the Johns Hopkins graduate school and also helped him to secure an assistantship there, a post which he entered upon in the autumn of 1900.

At Johns Hopkins, David Tennent was one of the group of keen and alert young men who came under the rigorous mental discipline and stimulating influences of Professors William Keith Brooks and Ethan Allen Andrews. As students, they were expected to meet the highest standards of intellectual achievement and their interests were roused in every aspect of biological knowledge and inquiry; as assistants, they were expected to fulfill their duties with accuracy and dispatch. In

recalling these student days with those who had shared them with him, Dr. Tennent would often chuckle over the devices which they used and the extent to which they went to collect the material Professor Brooks wanted for his classes. If Professor Brooks gave instructions that certain specimens were to be ready at a stated hour in the morning, they had to be ready and in good condition at that moment, even if the orders meant that his assistants spend the night scurrying through the city of Baltimore and its outskirts, searching ponds and streams, rain-water barrels and water butts for the particular kind of alga or rotifer demanded, with complete disregard for weather, property rights and time but that of the hour when the specimens must be on hand in the professor's laboratory.

The summers of those student years were spent at the Fisheries Laboratory, Beaufort, North Carolina, where with others of the Johns Hopkins group, David Tennent studied the marine flora and fauna of that strip of the Atlantic coast, collected, fished, swam and sailed by day, and by night sat on the broad porch of the laboratory building, looking out over the sea and discussing topics that ranged from practical and theoretical biology to politics, sociology, philosophy and religion. He took one year from his graduate work to substitute at Randolph Macon College, where he was appointed Acting Professor of Biology and Physics. In 1904, he received the degree of Doctor of Philosophy from Johns Hopkins, having held the honored Bruce Fellowship there and been elected to Phi Beta Kappa in his last student year. His doctoral dissertation was "A Study of the Life-History of *Bucephalus haimeanus*: A parasite of the oyster."

In the autumn of 1904, with his new degree and the stimulus of his Hopkins' days fresh upon him, he began his first term of appointment at Bryn Mawr College. First as an Instructor, then as Associate, Associate Professor, and Professor, he taught there for thirty-four years. There he met, and in 1909 married, Esther Margaret Maddux, and together they set up their home in the village of Bryn Mawr and became as much a part of the community in which they lived as they were of the college where he taught and where she had been a student. Their only child,

David Maddux Tennent, now a research biochemist, was born in 1914. Although Dr. Tennent held continuous appointment to the faculty of Bryn Mawr College from 1904 to 1941, his teaching and research were by no means confined to its classrooms and laboratories. The summer of 1909 was the first of many that he spent at the Biological Laboratory of the Carnegie Institution in the dry Tortugas of which Dr. Alfred G. Mayor was founder and director from 1904 until his death in 1922. Dr. Tennent was Executive Officer of this laboratory from 1937 until it closed in 1940. In 1911 he worked at the temporary station established by the Carnegie Institution at Montego Bay, Jamaica, B.W.I.; he worked, too, at various times at the Zoological Station in Naples, Italy, the Hopkins Marine Station at Pacific Grove, California, and the laboratory of the Carnegie Institution at Cold Spring Harbor, Long Island. He spent several summers at the Marine Biological Laboratory at Woods Hole, Massachusetts, where from 1920 until 1923 he directed the course in embryology. In 1913, on special leave of absence from Bryn Mawr, he went to Torres Strait and Thursday Island in the South Pacific as a member of an expedition of the Carnegie Institution of Washington under the direction of Alfred G. Mayor; his former professor, Hubert Lyman Clark, was also one of its members. In 1922-23, on sabbatical leave, he went to the Imperial University of Tokyo's Laboratory at Misaki, Japan, and his last leave, in 1930-31, was spent as visiting professor at Keio University in Tokyo.

The first visit to Japan was marked by tragedy. Toward the end of the summer of 1923 he, his wife and son went to China for a brief holiday before returning home. Always a cautious man, Dr. Tennent took care to leave his scientific equipment, the material he had collected and most of his notes secure, as he thought, in the vaults of a Tokyo bank. On the way back to Japan, their ship received the news of the earthquake that on September first had shaken Tokyo and Yokohama. The bank building, together with his material, was destroyed, and though he later published some of the results of this year's work from the fragmentary notes he had kept with him, its full value was never realized and his disappointment over the loss was never

mitigated. This experience left its mark upon him and made him even more cautious than before. For years afterwards he kept his brief case with his current notes and papers always with him, leaving nothing that could not be duplicated or replaced in the laboratory over night, or even during his absence by day unless put in charge of someone to rescue it in case of accident.

All the influences of his student days had conspired to make him a marine biologist, and the eagerness with which he embraced pure science, once the opportunity was given him, and turned to the study of animals of the seacoast for the solution of fundamental problems of biology belies his own admission of regret for the medical career denied him. To many his name is associated especially with the development and structural characteristics of the echinoderms, for they, particularly the sea urchins, provided the material used most extensively in his studies. But the processes that he investigated in them were ones whose interpretation had implications and applications far beyond the confines of any particular phylum. His early work was concerned primarily with the role of the nucleus in differentiation and development, a problem that he approached through a study of hybrids obtained by cross-fertilizations of different species, different genera, different orders and even different classes. These studies on echinoderm hybridization, which are accepted as biological classics, led him, in the logical sequence that he valued so much, to those on the fertilization process and so to investigations of the nature of the cell membrane, the potentialities of egg fragments, the morphological and biochemical organization of the echinoderm egg, and, finally, to the studies of photosensitization upon which he was engaged at the time of his death.

When David Tennent finished his graduate studies and began his own independent investigation, the mendelian theory of inheritance was new, and the chromosomal mechanism of mendelism was just coming into prominence; the contributions of the egg and the sperm to the establishment of the characters of the embryo and the relative roles of nucleus and cytoplasm in differentiation and development were problems in the forefront

of biological inquiry. Tennent's visits to marine laboratories in many parts of the world gave him opportunity to determine the chromosomal complement and to study the normal development of many different species of sea urchins. It was this familiarity with the conditions of their development in nature and under standardized conditions in the laboratory that enabled him to establish definite, objective criteria for variations in the hybrids he obtained and to determine the fate of individual chromosomes in the hybrid nucleus. By careful studies of the number of chromosomes and their configurations at anaphase, carried on by himself and his students, he distinguished the autosomes and sex chromosomes of a number of different species, and established the fact that the male is the digametic sex in sea urchins. Thus, when he fertilized the eggs of *Toxopneustes* (*Lytechinus*), in which the X chromosome is V-shaped, with sperm of *Hipponoë* (*Tripneustes*) in which it is J-shaped, approximately  $\frac{1}{2}$  the fertilized eggs contained the J-shaped element and  $\frac{1}{2}$  lacked it. Since the J-shaped chromosome was peculiar to *Hipponoë* and never found in species-fertilized *Toxopneustes* eggs, it could only have been introduced into the hybrid by the *Hipponoë* sperm. Since it was found in only 50% of the fertilized eggs, it must have been absent in 50% of the sperm used in the hybridization experiment, thus proving that the male was digametic.

Much of his early work was concerned with the relative contribution of the egg and the sperm in the determination of embryonic and larval characters, for to him "one of the most interesting and important problems connected with the results of Echinoderm hybridization is the determination of the factors influencing the appearance of maternal or of paternal characteristics in the hybrid embryo" (1910). For example, fertilization of the eggs of a Mediterranean species of *Sphaerechinus*, that produces functional gametes throughout the year, with sperm from *Strongylocentrotus*, if made in May, June or July, gave larvae of the *Sphaerechinus* type, while the same cross made later in the year yielded larvae resembling *Strongylocentrotus*, the sperm-contributing parent. The dominance of one parent over the other was in these crosses determined by the char-



acteristics of the larval skeleton, a feature which he had accepted as the most constant after a detailed study and statistical analysis of the variations ordinarily occurring in larvae from species-fertilized eggs raised under carefully standardized laboratory conditions. Tennent found in *Hipponoë-Toxopneustes* crosses, that in ordinary sea water, or sea water made slightly alkaline, the larvae of reciprocal crosses were of the *Hipponoë* type, while in sea water in which the  $H^+$  concentration was increased by the addition of HCl or acetic acid the larvae were of the *Toxopneustes* type. He suggested that the seasonal variations in the larvae obtained by other workers might be the result of naturally occurring changes in the  $H^+$  concentration of the environment of the parents and of the cleaving eggs from which the larvae were derived. His emphasis at that time on the importance of extrinsic influences upon the development of the individual and of an "optimum" for normal developmental processes has received ample support from more recent genetic and embryological studies.

On the premise that sperms differ in the degree of their effect upon the egg, and that the activating potency of a sperm could be supplemented by "increasing or diminishing its task," Tennent experimented with the effect of exposing eggs before cross-fertilization to monovalent cations, presumed to increase the permeability of protoplasm to water and ions, and to bivalent and trivalent cations, presumed to decrease its permeability. Using in one set of experiments sea urchins of different families (*Heliocidaris* and *Temnopleurus*) and in another those of different orders (*Heliocidaris* and *Astriclypeus*), he found that after treatment of the *Heliocidaris* eggs with NaCl, 90% of the eggs inseminated with *Temnopleurus* sperm formed fertilization membranes and underwent regular cleavage, and that with treatment with  $CaCl_2$ ,  $BaCl_2$  or  $SrCl_2$ , 100% of the *Heliocidaris* eggs exposed to the sperm of *Astriclypeus* formed perfect membranes and segmented regularly. His criterion of successful fertilization in these crosses was the elevation of the fertilization membrane and, in those cases in which it could be followed microscopically in the living egg, the union of egg and sperm nuclei. His intention was to check on nuclear

fusion in all the inseminated eggs, and so to rule out the possibility of parthenogenesis, but these experiments were carried out at the Misaki Marine Biological Station and the material he had preserved for future study was part of that lost in the Tokyo disaster. Later, similar experiments on the eggs of *Tripneustes* and *Lytechinus* confirmed those on *Heliocidaris*; he found, indeed, that with proper treatment the *Lytechinus* egg could be brought to a condition in which it was more readily activated by foreign sperm than by that of its own species. These experiments demonstrated the specificity of sperm in the activation of eggs of their own species, a condition which had been accepted but not established; also the difference in degree of their effect upon eggs of other species, and the role of the ionic concentration of sea water in controlling or directing that effect.

Perhaps the most significant of his studies on echinoderm hybridization were those in which he determined the time at which the influence of the paternal chromosomes first manifests itself in the embryo, and those in which he proved that the chromosomes eliminated during the cleavage of cross-fertilized eggs were of paternal origin. By crossing species that differed not only in the tempo of cleavage but in such clear-cut features as the time and site of mesenchyme formation, he was able to produce definitive evidence of the maternal control of early developmental processes and the later effect of the paternal determiners. He fertilized, for example, the eggs of *Cidaris*, a primitive species in which cleavage is slow and the mesenchyme appears after the formation of the archenteron, with sperm from *Lytechinus*, a species in which cleavage is completed in about one-third the time of cleavage in *Cidaris* and the mesenchyme begins to invade the blastocoele at the very onset of gastrulation. These differences between the two species were so evident that there could be no doubt that the cross-fertilized *Cidaris* eggs segmented at the *Cidaris* tempo and that the time of appearance and the location of the first mesenchyme cells in the hybrid embryo were *Lytechinus* in character. Tennent's results were more exact than those of Driesch and others who had studied the same problem but had chosen less well-defined

and more variable characteristics, such as larval shape and the total number of mesenchyme cells formed, as criteria of maternal or paternal influence. In these studies, as in those on the elimination of chromosomes from the hybrid nucleus, it was his detailed knowledge of echinoderm cytology that enabled Tennent to answer questions still puzzling others, and to provide definitive proof for certain points about which existing evidence was questionable or conflicting.

Although a number of workers had observed the elimination of chromosomes from the spindles of the early division figures of cross-fertilized eggs, some confusion existed as to the source of the eliminated chromosomes. It was through his knowledge of the details of chromosome configuration in the species crossed that Tennent was able to establish the fact that it was chromosomes of paternal origin, rather than of maternal, that lagged on the spindle and were ultimately eliminated from the hybrid nucleus. In consequence he added another category, "partial hybrids," to the other two, true and false hybrids, proposed in 1918 by Günther Hertwig. Among true hybrids were included all those with complete sets of maternal and paternal chromosomes; among false, those, essentially parthenogenetic in their development, in which the maternal chromosomes alone were retained; Tennent's partial hybrids in which there was a partial elimination of chromosomes of the paternal set might be fertile, sterile, misformed or non-viable individuals. This elimination of chromosomes, and other disturbances of development, apparent in some hybrid embryos, he interpreted as a disorganization of the orderly series of developmental reactions taking place in species-fertilized eggs brought about by the introduction of foreign nuclear material. He therefore proposed that the term "internal block," in current use to designate any check in the series of reactions that make up the fertilization process arising after the successful penetration of the sperm, be restricted to conditions inhibiting the union of the egg and sperm nuclei, and that the term "developmental block" be used for conditions inhibiting normal development after such union. The "developmental block" in hybrids obtained by fertilizing *Cidaris* eggs with sperm from either

Lytechinus or Tripneustes, an interordinal cross, is apparent in the gastrula stage of the hybrid embryos and represents, according to his interpretation, the expression of divergence of the two paths of development characteristic, on the one hand, of the maternal species and, on the other, of the paternal. Emphasizing again that what is transmitted from parent to offspring is a potentiality of development, rather than fixed and specific characters, he pointed out that this development depends upon reactions between nucleus and cytoplasm, and upon adjustment to environmental conditions. From evidence obtained in crosses between *Arbacia* and *Moira* and between *Lytechinus* and *Tripneustes*, he concluded that foreign sperm brings about changes in the physical characteristics of the cytoplasm of the egg, possibly due to the action of foreign enzymes on the cytoplasmic substrates. His observations of the appearance and disappearance of basophilic material in the vicinity of the nucleus in the early cleavage stages of *Arbacia* eggs activated by *Moira* sperm, and his statements: "there is a distinct impression of diffusion from the nucleus"; and later, "the sections give the impression of a movement of some of the contents of the cell toward the nucleus"; and finally "the nucleus in cross-activated *Cidaris* eggs seems to be supplied with more material than it can utilize" were perhaps less significant thirty years ago, when he wrote them, than they are today, when so much of the attention of cytologists and cytochemists is focussed on the nucleic acid metabolism of the cell.

His interest in the chemical constitution of the cell was expressed in the analysis made under his direction of the alcohol-soluble components of the eggs of *Echinometra lucunter*, the reaction of the substances so extracted to standard histological fixation and staining procedures and the comparison of these reactions with those given by components in the cells of ovaries collected at the same time and preserved for cytological study. While this study was in progress, he was collaborating with C. V. Taylor and D. M. Whitaker in an investigation of the morphological organization of the egg of *Lytechinus variegatus*, and the developmental capacities of egg fragments. The eggs were fragmented by a microdissection technique, which made possible

the exact localization of the fragment removed, and subsequently fertilized by sperm of the same or different species. The transparency of these eggs, and an ingenious device of Taylor's, enabled the observers to keep the egg fragments under almost continuous observation and to make accurate records of the larval structures they formed.

It was in the course of these investigations that his attention was directed to the effects of sunlight upon the eggs of *Lytechinus* stained with neutral red, a dye which, non-toxic to the cells in the dark or in moderate diffuse light, became toxic after exposure to the direct rays of the sun, a change presumably brought about by a compound formed from neutral red by a photochemical reaction. He planned an extensive program of research on the photodynamic effects of a wide range of non-toxic dyes exposed to different intensities of light. This promised to be the most valuable and the most significant of his studies, the culmination of all that he had learned about the cell in growth and division, for he saw in it the possibilities of an interpretation of the complex processes of typical and atypical growth. Although he had assembled the data of a long series of experiments, he died before he had completed his interpretation of them, and it is a loss to biological thought and progress that he had not time to put on paper the conclusions he had drawn from his study, the only record of which is in the memories of those with whom he had discussed them.

His published work is a succinct and critical exposition of his own and contemporary work, the logical development of ideas and evidence substantiating them, and much that is instructive in technique and stimulating to thought. His written words express the qualities of mind that characterized him as an investigator and as a teacher, and the standards and traditions of scientific work that he established for all with whom he came in contact as instructor, collaborator and fellow-worker constitute a great measure of his contribution to the progress of biological science. Professor Robert E. Coker, a friend and scientific companion since the days when they were students together at Johns Hopkins, said of him: "There was almost no waste effort in his research. He always had a signifi-

cant problem to begin with. A keen mind sensed the opportunity for crucial experiments; driving energy and intensive application carried the research through; comprehensive knowledge and broad vision enabled him to steer away from ready pitfalls; and, finally, a highly discriminating judgment, reinforced by basic integrity, saved him from conclusions that would require later revisions by himself or others." To these characteristics of his research might be added the meticulousness and precision of his techniques, the thoroughness with which he worked at a problem and the pertinacity with which he returned again to points in procedure or in deduction with which he was not wholly satisfied. These were the qualities that made his work so sound and so enduring, but robbed him of the wider fame he might have had, for he chose to answer questions rather than to raise them, and his work is characterized more by its completeness than by controversial issues opened or new lines of thought developed.

That his research was highly valued during his life is attested by the increasing opportunities given him to broaden it and to carry it further afield, and by the scientific honors that came to him. Dr. Tennent was President of the American Society of Zoologists in 1916, and of the American Society of Naturalists in 1937. He was elected to the National Academy of Sciences in 1929 and in 1938 was made a member of the American Philosophical Society. He was an active member of all the organizations to which he belonged, as he was of the faculty in which he held appointment, taking his full share of committee work and performing it with the diligent conscientiousness that was characteristic of all that he did.

His whole life was one of diligence, industry and perseverance. In his research, in his teaching, in his administration, and in his dealings with other people he was a perfectionist. In all that he did he set himself the highest goals and took pride in attaining them. It was his boast that he never came to a decision without ascertaining all the available facts in the case, duly weighing the evidence and finally coming to an impartial and objective judgment. If his deliberation sometimes made those who worked with him impatient, they were bound to

respect the honesty and sincerity of his final word. He was a severe critic of his own observations and conclusions, weighing them always in relation to the implications of the work of others, and he adhered strictly to his own exacting standards in research and publication. In the conduct of his life as in that of his experiments he was a scientific realist; he could not go beyond the evidence and once he had drawn his conclusions from it, clung to them with a tenacity that at times bordered on stubbornness.

During his teaching years he trained many undergraduate and graduate students, preparing them for advanced study, for research and for teaching. Twelve students, alumnae of other colleges as well as of Bryn Mawr, completed their work for the doctorate under his direction. To his students he was a kind friend, and in the tradition of his own student days, an exacting instructor. His own standards of intellectual integrity, of industry and accuracy in all that he said and did were so high that he expected the same of others but he never asked more of them than he did of himself. He was impatient with superficiality and intolerant of indolence, but patient beyond most with honest effort, however unsuccessful. He was a man of few words, but those he did speak were apt and well-timed; he knew when to encourage his students, when to ignore and when to chasten them. On the occasions when even his patience was exhausted by the perversity of objects or the carelessness or stupidity of individuals he could give way to bursts of anger so real that those who witnessed it were not apt to forget it nor the incident that had aroused it. Both by precept and example he was a good teacher; anyone who was under his instruction could hardly fail to appreciate and to value the quickness with which he perceived and the clarity with which he presented the essence of a subject, the precision and deftness of his laboratory technique, the comprehension and skill with which he planned a course of action, the patience and persistence with which he followed it, and, above all, the pure delight that he felt in scientific research.

Professor Tennent ended his active teaching at the close of the academic year 1937-38, having reached the age of obligatory

retirement. But he felt himself vigorous and alert and far from desirous of abandoning either teaching or research or indulging in the leisure he had so amply earned. He was moreover deep in the study of some of the material that he had prepared during his last summer in the Tortugas which he would have found difficult to continue outside of a laboratory. Fortunately it became possible for the college to offer him a research professorship, and it was as their first research professor that he continued his work. He was in his laboratory throughout the day before his sudden death on January 14, 1941.

In the administration of his department he was fair, wise and far-sighted. To his staff he was generous and just, an ambitious yet provident leader; he defended their rights, shared their personal and professional happiness and disappointments, counselled and encouraged them. If criticism or censure was necessary, he felt it his responsibility to give it, and never evaded what he considered his duty, however unpleasant it might be to him. He insisted that everyone associated with him have time and opportunity for research and felt an almost personal gratification in the achievements of his staff. Believing in the unity of science, he emphasized in his teaching and his administration the interrelationship of all the natural sciences and developed in his department the borderline fields of biochemistry and biophysics. It was largely due to his thinking and his efforts that a plan for coordinated teaching in the natural sciences was in 1935 instituted at Bryn Mawr, supported by a fund given by the Carnegie Corporation of New York. Under this plan, students with basic training in two or more of the natural sciences are enabled, as advanced undergraduates or as graduates, to continue their studies under the joint direction of two departments, and to become familiar with the problems and methods and be trained in the techniques of more than one field of specialized knowledge.

He was a valued, respected and much-loved member of the faculty to which he belonged. Bryn Mawr College was but twenty years old when he came to it, and he early identified himself with those on its faculty who worked for liberal policies in teaching and in administration. He was one of a group of



faculty members who drew up the "Plan of Government" upon which the college has operated since 1916 and which, based on the principles of democracy, provides for faculty representation on college committees and faculty cooperation in the problems of administration. He himself served faithfully on nearly all the committees that he had helped to set up, giving his time to them fully and efficiently. He was a man in whose kindness, fairness and rightness of opinion every one had trust; though rigid in his beliefs and firm in his convictions, he was able to see both sides of a question and to give dispassionate judgment, even though in his kindness and friendliness he might deplore the decision and secretly suffer because of it. His colleagues and his students had confidence not only in his wisdom but in his fairness. He paid the price of that confidence and trust in the heavy load of committee work that was asked of him both by the college and the organizations to which he belonged, and the frequency with which others turned to him for advice and help when they were in difficulties.

He was no scholarly recluse, shut off from others and the affairs of the world around him. He and his wife delighted in the society of their friends, and their house was a place where many were welcomed with genuine friendliness and warm-heartedness. Though he was formal in his manner and gave the impression of shyness, he was a gracious host and took evident and genuine pleasure in providing his guests with the best that he could offer, whether of food or drink or entertainment. He followed with enthusiasm the course of his son through school and college, sharing with him the excitement of football and baseball games, plays and dances. He regretted the increasing informality of daily life and was always most punctilious in his social relations; he confessed that one thing that pleased him about his appointment to Keio University in 1930 was that he would once again have the opportunity to wear a top hat as a matter of course on appropriate occasions. He was good company, for he was an excellent raconteur, with a fund of stories, some of them of his student days, some of them of his adventures in the many places where his work or his pleasure took him, and some of them garnered from his

wide and cosmopolitan circle of friends. He loved to share a good story as he loved to share a good book or an experience that he had found especially interesting or otherwise satisfying. Few of those who knew him well and heard him tell of his experience in the South Pacific can see a picture of the Great Barrier Reef without projecting into it an image of his short and rather stocky figure, intent upon the observation of the sea creatures living there whose form and origin and behavior fascinated and puzzled and charmed him. But besides vividness, his stories had spice and humor; often beginning them with a shy and tentative smile, he would end them shaking with the laughter that he would have restrained if he could.

He was as much a figure and influence in the community where he lived as he was in the college where he taught. His advice was sought on local affairs and he always had time to give it judicially, as he always had time to chat for a minute or two, on his way back and forth between his home and the college, with his friends at the bank, the lumber mill and the drugstore. There were often fishing parties with this circle of friends as well as expeditions to the Philadelphia baseball parks where the fortunes of the American and National League teams were followed with keen interest and obvious enjoyment. Later, he began to play golf and in the last years of his life nearly every Sunday morning saw him on the links, even in weather which defied younger and more vigorous men.

He was loved, he was respected, he was honored, and his life was full of the satisfactions that come from the knowledge of work well done and of purpose achieved. He never failed to have a kind of boyish pleasure in gaining an objective he had decided upon and a genuine intellectual satisfaction in seeing a carefully thought out plan gradually unfold itself to the end he had intended. Though he was a modest man, he did not underestimate the standard of values he had set for himself or his own accomplishments. And he was fortunate in knowing during his life, from the tributes that were paid him, the affection and esteem in which he was held by others and the respect he had inspired as a man and a scientist. He had all the qualities that make the scientist,—the driving curiosity about objects and

events in the natural world, the urge to experiment with them, the complete integrity and critical objectivity that scientific analysis demands ; but he also had, in greater measure than most, those other attributes that mark the best among men and the best among scientists—simplicity before men and humility before God. His death was a sad loss to the college that he served and to the science that he loved.

BIBLIOGRAPHY

KEY TO ABBREVIATIONS

- Amer. Nat. = American Naturalist.  
Arch. Entw.-Mech. = Archiv für Entwicklungsmechanik der Organismen.  
Biol. Bull. = Biological Bulletin.  
Carnegie I.W. Publ. = Carnegie Institution of Washington, Publications.  
Tortugas Laboratory.  
Carnegie I.W. Yr. Book. = Carnegie Institution of Washington, Year  
Book. Tortugas Laboratory.  
J. Exp. Zoöl. = Journal of Experimental Zoölogy.  
J. Morphol. = Journal of Morphology.  
Proc. Nat. Acad. Sci. = Proceedings, National Academy of Sciences.  
Proc. 7th Int. Zoöl. Cong. = Proceedings, Seventh International Zoölogical  
Congress.  
Q. J. Micros. Sci. = Quarterly Journal of Microscopical Science.

1906

- (With M. J. Hogue.) Studies on the development of the starfish egg.  
J. Exp. Zoöl., III, no. 4, pp. 517-541, 5 pl.  
A study of the life-history of *Bucephalus haimeanus*; a parasite of the  
oyster. Q. J. Micros. Sci., XLIX, pt. 4, pp. 635-690, pl. 39-42.

1907

- Further studies on the parthenogenetic development of the starfish egg.  
Biol. Bull., XIII, no. 6, pp. 309-316, 14 figs.  
Hybrid echinoderm larvae. Proc. 7th Int. Zoöl. Cong., pp. 519-520.

1908

- The chromosomes in cross-fertilized echinoid eggs. Biol. Bull., XV, no. 3,  
pp. 127-134, 1 pl., 12 figs.

1909

- An account of experiments for determining the complete life-history of  
*Gasterostomum gracilescens*. Science, n.s., XXIX, no. 741, pp. 432-433.  
Experiments in echinoderm hybridization. Carnegie I.W. Yr. Book, no. 8,  
pp. 136-138.

1910

- (With V. H. Keiller.) The anatomy of *Pentaceros reticulatus*. Carnegie  
I.W. Publ., no. 132, pp. 111-116, 3 pl., 2 text cuts.  
The dominance of maternal or of paternal characters in echinoderm  
hybrids. Arch. Entw.-Mech., XXIX, 1, pp. 1-14, 2 figs.  
Echinoderm hybridization. Carnegie I.W. Publ., no. 132, pp. 117-151,  
6 pl., 7 text cuts.

Experiments in echinoderm hybridization. Carnegie I.W. Yr. Book, no. 9, pp. 134-135.

Variation in Echinoid plutei; a study of variation under laboratory conditions. J. Exp. Zoöl., IX, no. 4, pp. 657-714, 21 figs.

1911

A heterochromosome of male origin in Echinoids. Biol. Bull., XXI, no. 3, pp. 152-154, 3 figs.

1912

The behavior of the chromosomes in cross-fertilized echinoid eggs. J. Morphol., XXIII, no. 1, pp. 17-25, 2 pl.

The correlation between chromosomes and particular characters in hybrid echinoid larvae. Amer. Nat., XLVI, pp. 68-75.

Investigations on the hybridization of Echinoids. Carnegie I.W. Yr. Book, no. 11, pp. 152-153.

Studies in Cytology: I. A further study of the chromosomes of *Toxopneustes variegatus*; II. The behavior of the chromosomes in *Arbacia-Toxopneustes* crosses. J. Exp. Zoöl., XII, no. 3, pp. 391-405, 3 pl., 21 figs.

1913

Echinoderm hybridization. Science, n.s., XXXVII, no. 953, pp. 535-537.

1914

The early influence of the spermatozoön upon the characters of echinoid larvae. Carnegie I.W. Publ., no. 182, pp. 127-138, 11 text-figs.

1920

Evidence on the nature of nuclear activity. Proc. Nat. Acad. Sci., VI, no. 4, pp. 217-221.

1922

Studies of the hybridization of Echinoids, *Cidaris tribuloides*. Carnegie I. W. Publ., no. 312, pp. 1-42, 3 pl., 28 figs.

1924

Investigations on the hybridization of Echinoids conducted at the Misaki Marine Biological Station of Tokyo Imperial University, from April 24 to August 16, 1923. Carnegie I. W. Yr. Book., no. 22, pp. 169-171. (With C. V. Taylor.) Preliminary report on the development of egg fragments. Carnegie I. W. Yr. Book, no. 23, pp. 201-206.

Specificity in fertilization. Science, n.s., LX, no. 1546, pp. 162-164.

1925

Investigations on specificity of fertilization. Carnegie I. W. Yr. Book, no. 24, pp. 240-242.

1926

(With C. V. Taylor and D. M. Whitaker.) Investigation on organization of echinoderm egg. Carnegie I. W. Yr. Book, no. 25, pp. 249-255.

1928

Microscopic investigation of the fixing and staining reactions of substances extracted from the eggs of *Echinometra lucunter*. Carnegie I. W. Yr. Book, no. 27, pp. 339-351.

1929

Activation of the eggs of *Echinometra mathaei* by sperms of the crinoids *Comatula pectinata* and *Comatula purpurea*. Carnegie I. W. Publ., no. 391, pp. 105-114, 5 text-figs.

Early development and larval forms of three Echinoids of the Torres Strait Region. Carnegie I. W. Publ., no. 391, pp. 115-118, 15 text-figs.

(With C. V. Taylor and D. M. Whitaker.) An investigation on organization in a sea-urchin egg. Carnegie I. W. Publ., no. 391, pp. 1-104, 59 text-figs.

1931

(With M. S. Gardiner and D. E. Smith.) A cytological and biochemical study of the ovaries of the sea-urchin *Echinometra lucunter*. Carnegie I. W. Publ., no. 413, pp. 1-46, 7 pl.

1933

Experimental studies in the embryology of Echinoids, particularly *Clypeaster rosaceus*. Carnegie I. W. Yr. Book, no. 32, p. 265.

1935

Investigations on the photodynamic properties of vital dyes. Carnegie I. W. Yr. Book, no. 34, pp. 91-92.

The photodynamic effects of vital dyes on fertilized sea-urchin eggs. Science, n.s., LXXXII, no. 2139, p. 621.

1936

The effect of irradiation of eggs of *Lytechinus* with sunlight during development in various dyes. Carnegie I. W. Yr. Book, no. 35, pp. 93-96.

1937

The effect of irradiation of *Lytechinus* eggs in various dyes with sunlight. Carnegie I. W. Yr. Book, no. 36, pp. 106-107.

1938

The effect of intensity of light on photodynamic reactions. Carnegie I. W. Yr. Book, no. 37, pp. 102-103.

Some problems in the study of photosensitization. *Amer. Nat.*, LXXII,  
pp. 97-109.

1939

The photodynamic effect of dyes on the eggs of *Lytechinus variegatus*.  
*Carnegie I. W. Yr. Book*, no. 38, pp. 231-233.

1941

(With Toshio Ito.) A study of the oögenesis of *Mespilia globulus*  
(Linné). *J. Morphol.*, LXIX, no. 2, pp. 347-404, 12 pl.

1942

The photodynamic action of dyes on the eggs of the sea-urchin, *Lytechinus*  
*variegatus*. *Carnegie I. W. Publ.*, no. 539, pp. 1-153, 8 pl., 40 text-figs.