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1872—1954

A Biographical Memoir by
GILBERT M. SMITH

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C E Allen

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CHARLES ELMER ALLEN, the only son of Charles and Eliza (North) Allen was born on October 4, 1872. His father was a native of New York, who moved to Wisconsin when a young man. There, for the first few years he taught school and eventually became Superintendent of Schools in Dodge County. He married Eliza North, daughter of a pioneer family of Fond du Lac, Wisconsin. While serving as Superintendent of Schools, he "read law" in the office of a lawyer in order to qualify for admission to the bar. From 1870 until his death in 1890 he practiced law in Horicon, Wisconsin.

At the time the Allens' son Charles was born, Horicon was a country village of a few hundred inhabitants; but in spite of its small size it had a high school as well as a grammar school. Here, Charles and his sister Florence received their secondary education, Charles was a studious youth, who graduated from the local high school at the age of 14. His sister writes: "As a boy he was an inveterate reader. I can remember him lying on the floor on his stomach, poring over books by the hour."

Charles did not enter the University of Wisconsin until three years after he graduated from high school. It seems safe to assume that his parents thought him too immature to enter college immediately after his preparatory work was completed at the age of 14. Accordingly, Charles returned to high school to study German and zoology. The latter was of special interest to him and his room

at home became filled with jars of specimens that he collected in the area adjacent to Horicon.

The year before starting work at the University was spent teaching all grades in a one-room country school. This was in an era when youths the age of their sixteen-year-old teacher attended country school and when the problem of discipline was a difficult one. The manner in which young Charles met this problem is unknown. That he met it successfully is shown by his being invited to continue for another year.

In the autumn of 1889 Charles matriculated at "Madison College," the name in general usage at that time for the University of Wisconsin. Within a few months his university career was interrupted because of the death of his father and the necessity of helping support his mother and sister. The judge of the circuit court promised Charles an appointment as assistant court reporter if he would prepare himself for the position. Accordingly, he went to Milwaukee to take private lessons from an experienced reporter. Within a few months he had acquired sufficient technical ability to qualify.

After six years as a full time reporter, Allen re-entered the University of Wisconsin. Here he supported himself by part-time work as a court reporter. In spite of this he was active in undergraduate activities. He was co-founder and first editor of *Sphinx*, the undergraduate humor magazine; chairman of the editorial board of the junior annual, the *Badger*; and editor-in-chief of the student newspaper, the *Cardinal*. All these publications are still flourishing under the same names at Wisconsin. Allen was also active in student debating societies and was on intercollegiate debating teams.

When Allen re-entered Wisconsin, Charles R. Barnes was Professor of Botany. Barnes had two fields of research activity; the physiology of plants and the taxonomy of bryophytes. Allen became especially interested in the latter subject but his only published investigation in the field is a short paper on the liverworts of the Apostle Islands in Lake Superior. At the beginning of Allen's senior year Barnes had resigned to accept a professorship at the

University of Chicago, and had been succeeded by Robert A. Harper. Harper, who had received his doctorate in Germany under the renowned Strasburger, was primarily interested in cytology. This interest in cytology was transmitted to Allen and for many years all his research activity centered around this area.

Immediately after receiving his baccalaureate Allen enrolled as a graduate student in botany at the University of Wisconsin. For the first two years he was an assistant in the department. In the middle of the summer session in 1901, H. G. Timberlake, an instructor in the department, was killed in an accident and Allen was asked to carry on his classes for the remainder of the session. The following autumn he was appointed to the instructorship formerly held by Timberlake. Upon receiving the doctorate three years later, Allen was appointed assistant professor, and in 1907 he was made an associate professor. A full professorship came in 1919, and he held this position until he became emeritus in 1943.

When Harper left Wisconsin to become Professor of Botany at Columbia in 1911, Allen succeeded him as chairman of the department. Under his chairmanship the department was run as a democracy and not as an autocracy. As a believer in democracy, Allen proposed that departmental chairmen should be elected by members of departments instead of being appointed by the University administration. When this proposal was adopted by the faculty and the chairmanship first became elective, he was the unanimous choice of the department. This he declined because of his sponsorship of the proposal. Other university duties included membership on several faculty committees. One of the most arduous of these was the Student Life and Interest Committee, on which he served for twenty years and for a few years he was its chairman.

Services outside university duties included membership in the National Research Council for many years and chairmanship of its Division of Biology and Agriculture for the fiscal year 1929-1930. From 1918 until 1926, Allen was editor of the *American Journal of Botany*, sponsored by the Botanical Society of America. He was a

most conscientious editor, and many an evening at home was spent carefully editing manuscripts or laboriously reading proofs. Other editorial duties included the editorship of the *Wisconsin Alumni Magazine* for its first three years (1899-1902) and editorship of the *Transactions of the Wisconsin Academy of Science, Arts and Letters* for two years.

A grant from the Carnegie Foundation enabled Allen to spend the academic year of 1904-1905 abroad. For most of the time he worked in the laboratory of Strasburger at Bonn, but a portion of the time was spent at the Naples Biological Station. This year in Europe, the year at Washington, and a semester as visiting professor at Columbia in 1904 were the only times that Allen was away from the campus when the University of Wisconsin was in session.

In 1920 six members of the Department of Botany at Wisconsin began the joint writing of an introductory text in botany. Each author was assigned certain chapters. When a preliminary draft of each chapter was completed, a copy was submitted to each of the co-authors and then the group met together for discussion of the manuscript. It was in these conferences that Allen's abilities as a scientist, writer, and editor were clearly apparent. No matter what the field of botany, he was usually the first to point out inaccuracies of statement or too broad generalizations. There were frequently divergent views as to how a matter should be stated. At times this led to long discussions, with a tendency for the occurrence of that academic occupational disease of wandering from the point. It was usually Allen who brought the discussion back to the point and who proposed a statement satisfactory to all. More frequently than others he was the one who pointed out ambiguities or statements that might be open to misinterpretation. Thus, whatever the merits the book possesses are due in large part to Allen's influence.

During his long career at Wisconsin, Allen taught a wide variety of courses. The course on cytology, which he taught until his retirement, and the one on heredity, which he gave for a number

of years before establishment of the Department of Genetics, were the two in which he took greatest delight. His approach to new discoveries, although distinctly conservative, was an open-minded one and he was willing to accept them as soon as he felt them definitely established. Allen's lectures were a marvel of exposition, with an immense amount of data presented with such clarity that the dullest student never lost track of the argument. His students appreciated his scholarly qualities but they also had a warm personal regard for him. Proof of this was to be seen when graduates returned to the campus, for the first place at which they called was Allen's office.

Allen was elected a member of the National Academy of Sciences in 1924. In 1941 he was granted an honorary Doctor of Sciences by the University of Chicago. The esteem in which he was held throughout this country is shown by his election to office in many scientific societies. He was president of the Botanical Society of America in 1921; the Wisconsin Academy of Sciences, Arts and Letters in 1931-1933; the American Society of Naturalists in 1936; and the American Microscopical Society in 1944. In 1928 he was vice president of the American Association for the Advancement of Science (Section G, Botany). Certain of these presidencies involved delivering an address upon assuming, or retiring from, office and these reveal the breadth of his biological outlook. Notable examples are "The Potentialities of a Cell" presented before the Botanical Society of America, and "Haploid and Diploid Generations" presented before the American Society of Naturalists.

The list of papers reporting the results of his investigations is not a long one. He did not publish until he thought he had a worthwhile contribution and he was not interested in accumulating a long bibliography. For the first decade and a half of his research career, attention was devoted exclusively to cytological problems. Almost all preparations were stained with the Fleming triple stain—a procedure in which it is exceedingly difficult to obtain a good percentage of properly stained preparations. He was a master of

this technique and in the laboratory in his course on cytology the students were required to master this technique even if it took them months.

The first of Allen's investigations was a study of development of the middle lamella between two recently divided cells. This demonstrated that the middle lamella may increase in thickness before deposition of secondary wall layers begins. During the next few years, investigations centered around problems of meiosis. The most notable of these was an attack on the problem of nuclear behavior during germination of the resting zygote of green algae. The difficulty in elucidating this problem was the finding of material whose zygotes could be induced to germinate and the obtaining of zygotes in sufficient numbers for embedding in paraffine, cutting in serial section, and staining. *Coleochaete* proved to be a green alga meeting these requirements, and an extensive series of stages in division of the nucleus of its zygote was obtained. Thus, for the first time, there was a demonstration that nuclear division in the resting zygote of a green alga is meiotic and not mitotic.

From about 1912 and throughout the remainder of his life, research activities centered around the bryophytes. This was a return to a field in which he had been interested during undergraduate days, but a return to different phases of bryology. The first two papers deal with spermatogenesis in the moss *Polytrichum*. They present a more detailed account of spermatogenesis than any previous study of it in mosses.

Even before the rediscovery of Mendel's laws became known, Allen had been interested in the operation of the hereditary mechanism. He followed the early development of the new science of genetics but did not begin investigation in that field until early in 1916. The problem selected was that of inheritance of characters in the gametophytic generation of bryophytes. This was a virgin field in which there had been no previous genetic studies in material grown from spores. His wide knowledge of bryophytes was of great value in the selection of material for experimentation.

The heterothallic (dioecious) liverwort *Sphaerocarpos* was chosen for study because it is one of the few bryophytes in which the four spores of a tetrad adhere to one another when mature. Study of the four gametophytes developing after the four spores of a tetrad have been dissected away from one another, makes possible a virtually immediate determination of the genetic effects of meiosis. A further advantage of *Sphaerocarpos* for genetic study is that a gametophyte derived from any spore may be propagated vegetatively and maintained in clonal culture for a number of years.

It is characteristic of the thoroughness of the man that the first step in the *Sphaerocarpos* project was a careful study of its cytology and of the morphology of development of its gametophyte and sporophyte. Cytological study resulted in the first discovery of sex chromosomes among plants. Those of *Sphaerocarpos* are of the XY type. The two sex chromosomes are markedly different in size and were shown to separate in the first meiotic division of a sporocyte nucleus. Of the four spores of a tetrad the two receiving the large X chromosome were found without exception to develop into female gametophytes and the two receiving the small Y chromosome to develop into male gametophytes.

For many years all available time was spent looking through a binocular dissecting microscope set up in the greenhouse. Sometimes this was for the dissection of spores, one from another, to obtain the four gametophytes derived from a tetrad. At other times it was the examination of gametophytes plant by plant in a search for mutants of a vegetative nature. At still other times it was a careful examination of crosses between two vegetatively different gametophytes. During the years there was a discovery of a number of mutations in vegetative characters of the gametophytic generation. The two that proved best for study of inheritance in gametophytes were "tuftedness," characterized by aberrancies in form of involucre around sex organs, and "polycladous," characterized by a profuse and irregular branching.

Crosses of mutants with typical gametophytes, as well as crosses

between two mutants, showed that vegetative characters are inherited in the same 1:1 ratio as is sexuality. None of the mutant characters was found to be borne on a sex chromosome, yet there was a certain amount of linkage of certain mutant characters with sexuality. This was explained by the assumption that certain chromosomes tend to be associated with the sex chromosomes during migration to the spindle poles during meiosis.

Another phase in the study of *Sphaerocarpos* was that of polyploidy. Gametophytes were found in which there was a chromosome complement of 14 autosomes and 2 sex chromosomes, instead of 7 autosomes and 1 sex chromosome. Diploid gametophytes in which the two sex chromosomes are X chromosomes were found to be female and with normal archegonia. Those with two Y chromosomes are male and with normal antheridia. Diploid gametophytes with one X and one Y chromosome are intersexes with both sex tendencies capable of expression but with the female tendency nearly, but not completely, in the ascendancy. The great majority of the sex organs borne by them were found to be of an intermediate type but more like antheridia than archegonia. In addition, there was a formation of some archegonia of normal appearance. Diploid gametophytes with two X or with two Y chromosomes form normal sex organs containing functional gametes. As a result, it was possible to obtain triploid and tetraploid sporophytes.

Sporophytes of *Sphaerocarpos* are so simple in structure that but little genetic study could be made of them. The one clear-cut character discovered was strain of *S. donnellii* in which the spores of a tetrad are not adherent. Cross matings with strains with adherent spores show that this sporophytic character is transmitted only through the female gametophyte and thus is a character carried by the X chromosome.

The last decade of Allen's life was marked by an increasing illness that made visits to his laboratory fewer and fewer. During the last three years of his life when he was unable to leave home, his interest in botany did not flag and he kept abreast of current de-

velopments through journals taken to him by colleagues. The end came on June 25, 1954.

In 1902 he married a classmate, Genevieve Sylvester of Milwaukee, Wisconsin. Mrs. Allen survives him, as do their three children, Edith (Mrs. C. R. Slater), Harold S., and Charles R. There are eight grandchildren.

In preparing this account of Professor Allen, I am indebted to his sister, Florence E. Allen, for information about his parentage and boyhood. Professor Richard I. Evans of the University of Wisconsin has furnished information on his early academic career and has prepared the bibliography of his publications.

KEY TO ABBREVIATIONS

- Am. J. Bot. = American Journal of Botany
 Am. Nat. = American Naturalist
 Am. Philos. Soc. Yearb. = American Philosophical Society Yearbook
 Ann. Bot. = Annals of Botany
 Ann. Bryol. = Annales bryologici
 Archiv Zellforsch. = Archiv für Zellforschung
 Ber. Deutsch. Bot. Ges. = Berichte Deutsche Botanische Gesellschaft
 Bot. Gaz. = Botanical Gazette
 Bot. Rev. = Botanical Review
 Bull. Torrey Bot. Club = Bulletin, Torrey Botanical Club
 Jahrb. Wiss. Bot. = Jahrbucher für Wissenschaftliche Botanik
 Mem. Brooklyn Bot. Garden = Memoirs of the Brooklyn Botanical Garden
 Proc. Am. Philos. Soc. = Proceedings, American Philosophical Society
 Proc. Int. Congr. Plant Sci. = Proceedings, International Congress of Plant Science
 Proc. Nat. Acad. Sci. = Proceedings, National Academy of Sciences
 Proc. Sixth Int. Congr. Genetics = Proceedings, Sixth International Congress of Genetics
 Trans. Wis. Acad. Sci. = Transactions, Wisconsin Academy of Sciences, Arts and Letters.

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