NATIONAL ACADEMY OF SCIENCES

RALPH ERSKINE CLELAND

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A Biographical Memoir by
ERIC STEINER

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BY ERICH STEINER

MUCH OF THE WORK that led to the establishment of genetics as a distinct biological discipline involved studies of *Oenothera,* the evening primrose. The concept of mutation, which remains central to the dogma of genetics, had its origin in the observations of Hugo deVries on *Oenothera.* deVries's mutation theory was challenged, however, when it became clear that *Oenothera* exhibited a breeding behavior that did not conform to that of other organisms. It took some thirty years before the genetic nature of *Oenothera* was fully explained. Ralph Cleland made a major contribution to the solution of this long-puzzling problem through his discovery of chromosomal ring formation at meiosis and the subsequent proof that it is the physical basis of the atypical breeding behavior of *Oenothera.*

Ralph Erskine Cleland was born in LeClaire, Iowa on October 20, 1892, the first child of Charles Samuel and Edith Collins Cleland. The family was of Scotch-Irish ancestry on both sides. Ralph's father, who spent his childhood on a farm in Minnesota, was a minister of the United Presbyterian Church; his mother came from a family of farmers in Ohio. When Ralph was one-and-a-half years old, his father accepted a call from a church in downtown Philadelphia, the pulpit of which he was to occupy for forty-five years. Charles

Cleland became active in denominational affairs, serving a term as moderator and spending many years as secretary of the Foreign Mission Board, an assignment that led him to travel extensively in Africa, the Middle East, and India.

Ralph grew up in a low-income, urban neighborhood where his playmates were largely children of factory workers. Ralph's father, however, insisted that the children spend their summers at a country cottage in Lehigh County, Pennsylvania. It was here that Ralph developed his interest in botany and natural history, spending much of his time roaming through the fields and woods.

In Philadelphia, Ralph attended Central High School where he was enrolled in the "classical" course. He considered his high school education unusual in that it was to some extent the equivalent of a college program. The curriculum was broadly liberal arts, the courses rigorous, and he was taught by men with recognized standing in their disciplines. He entered the University of Pennsylvania with a four-year scholarship, receiving advanced credit for some of his high school work. He selected classics as his major and history as a minor, but he also took several courses in botany. During his undergraduate years Ralph engaged in a number of extra-curricular affairs, including participation in plays, debating, sports, the editorial board of the yearbook, and membership in the literary society. He believed that the latter activity contributed in particular to his social development during the college years. Undergraduate honors included prizes in Greek and botany and election to Phi Beta Kappa.

In addition to his college studies and activities, he worked in the social programs of his father's church, an experience that impressed upon him the damaging social effects of alcohol and led him to become a lifelong teetotaler.

Upon graduation from the University, Cleland was offered an assistantship in the Department of Botany, even though his course preparation in biology was minimal. Nevertheless, by working summers, and with the aid of a Harrison Fellowship for two years, he was able to complete the requirements for the Ph.D. in three years. His doctoral research was carried out under the direction of Professor B. M. Davis, whose interests centered on cytological studies of the algae and the cytogenetics of *Oenothera.* Cleland chose to work on the cytological life history of a red alga, *Nemalion multifidum.* As a result, he spent his summers at Woods Hole where he was able to extend his acquaintance with other biologists. In July of 1918, upon mailing his thesis to be published, he returned home to find an order to report for induction into the military service. After five weeks of training, he was sent to France with a field artillery unit. Shortly after his arrival abroad, he was hospitalized with influenza. By the time he recovered, the armistice had been signed and he returned to the United States to be discharged from the army in April 1919.

Ralph Cleland's research career had its origin in a set of fortuitous circumstances. Shortly after his discharge from the army, he obtained an appointment as an instructor in biology at Goucher College, to begin in the fall of 1919. Without a commitment for several months, Cleland offered to assist Professor B. M. Davis with his research. Dr. Davis was at the moment interested in the cytology of the hybrid between a diploid and tetraploid race of *Oenothera* and turned the problem over to Cleland. Cleland chose *Oenothera franciscana,* a strain that happened to be at hand, for determining the best methods of fixation and staining. The study of *Oe. franciscana* proved to be of greater interest than a mere test of technique, since the cytological preparations revealed that four of the fourteen chromosomes regularly formed a closed circle at meiosis. This observation led to a series of studies by Cleland that were of major importance in elucidating the puzzling genetic behavior of *Oenothera,* a problem that had remained largely unsolved since it first came to light as a result of studies of the genus by Hugo deVries at the turn of the century.

Hugo deVries, a Dutch plant physiologist, initiated studies of variation in *Oenothera* in 1885, hoping to attack problems of evolution through an experimental approach. His results led to the publication in 1900 of *The Mutation Theory,** in which he proposed that evolution of new species occurred through sudden and spontaneous changes in one or more hereditary characters. Evidence for his theory came largely from observations of *Oenothera*; it was quickly apparent that the concept of mutation could only be valid if the strains alleged to be undergoing mutation were pure species. Were the strains of hybrid nature, then such variations, which deVries called mutations, could simply be recombinants. The problem arose because strains of *Oenothera* bred true when self-pollinated, but behaved as hybrids when outcrossed. It was thus essential to establish the purity of the *Oenothera* species before the mutation concept could be considered valid and thus significant for evolutionary theory.

The contradictory behavior of *Oenothera* remained a puzzle that attracted a great many investigators in the early 1900's, but their efforts met with little success until the meticulous genetic analysis of Otto Renner, published in 1917, which demonstrated that many of the oenotheras were permanent heterozygotes persisting in this condition because of balanced lethal factors. Ralph Cleland's study of *Oenothera franciscana* appeared in 1922 and was the first step toward the explanation of the physical basis of the mechanism revealed by Renner's brilliant analysis. The curious fact is that

* H. deVries, *Die Mutationstheorie* (Leipzig: Von Veit; vol. 1, 1901; vol. 2, 1903); *The Mutation Theory* (English translation, Chicago: Open Court; vol. 1, 1909; vol. 2, 1910).

numerous cytological studies of *Oenothera* had been carried out during the previous two decades, yet no one had recognized that the formation of chromosome rings at meiosis was an unusual and constant feature of most of the *Oenothera* strains under investigation.

The paper on *Oenothera franciscana* does not place emphasis on the discovery of chromosomal ring formation; more attention is focused on the evidence for the purity of *Oenothera franciscana* and the general importance of species purity for the *Oenothera* problem. The next paper published by Cleland appeared in the *American Naturalist* in 1923 and had an entirely different orientation. In the interim Cleland had examined the meiotic division in several other strains of *Oenothera* and discovered that each had a characteristic chromosomal configuration involving circles of various sizes. He noted that the adjacent members in a circle of chromosomes appear to go to opposite poles, an arrangement not likely to depend purely on chance. Further, if one assumes that homologous chromosomes go to opposite poles, then circle formation could explain the genetic results of Shull, who had concluded that all the genes in *Oenothera* belong to a single linkage group.

Cleland's studies of the following years extended the number of *Oenothera* strains examined. He established that a wide range of chromosomal configurations occur and each remains constant for a particular strain. Moreover, it was recognized that some mechanism must exist to give the regular arrangement of the chromosomes in the circle that leads to alternate segregation at the time of the division. Nevertheless, at this time Cleland still believed that the chromosomes in the circle were unpaired; thus he failed to recognize the cause of circle formation.

Not until the 1926 paper on meiosis in *Oenothera biennis* and *Oe. biennis sulfurea* did Cleland specifically cite Renner's work and utilize the balanced lethal concept to explain the genetic behavior of *Oe. biennis.* It is clear that by this time Cleland was fully aware of the direct relationship between the unique chromosomal situation and the atypical genetic behavior of *Oenothera*; a coherent hypothesis still remained to be developed, however.

The award of a Guggenheim Fellowship made it possible for Cleland, accompanied by his recent bride, Elizabeth, to spend the summers of 1927 and 1928 as well as the intervening academic year in Germany in collaborative efforts with Friederich Oehlkers, Otto Renner, and Hugo deVries. A major study aimed at correlating the chromosome configurations in various races of *Oenothera* and their hybrids with their breeding behavior was undertaken with Dr. Oehlkers. In this project Cleland assumed responsibility for the cytological work, while Oehlkers carried out the genetic studies. The preliminary results of the work were reported in the *American Naturalist* in 1929; this was followed by a full account in 1930 in the *Jahrbuch für Wissenschaftliche Botanik.* These articles presented convincing evidence that races of *Oenothera* exhibiting a circle of fourteen chromosomes at meiosis transmitted the genes in single groups; the hybrids, on the other hand, showed diverse configurations at meiosis, but with each hybrid constant in its configuration. Further, the number of linkage groups was shown to be precisely correlated with the number of pairs and/or circles of chromosomes at meiosis. Here was rigorous proof of the correlation between gene and chromosome behavior. While the breeding behavior of *Oenothera* could now be understood in terms of its unique chromosomal mechanism, questions regarding the nature and distribution of the chromosomes still needed to be answered. Cleland did not offer an explanation for the formation of the chromosomal circles. He continued to consider the chromosomes within a circle as essentially unpaired and as examples of telosynapsis (association of the ends of chromosomes), a concept that later proved to be incorrect.

The explanation for circle formation was first suggested by John Belling in a 1927 paper dealing with various types of chromosome configurations observed in *Datura stramonium*.* Among these was a circle of four chromosomes, the members of which could be identified morphologically and thus recognized as nonhomologous. Belling reasoned that an exchange between two nonhomologous chromosomes had occurred, and that such a plant, possessing two original chromosomes and two that had interchanged segments, would exhibit a circle of four chromosomes as a result of their pairing requirements. The concept of segmental interchange† was the element needed to solve the last major question of the *Oenothera* behavior.

Further, the concept of segmental interchange led Cleland to recognize that chromosome configuration could serve as an index of similarity in segmental arrangement, pairs or small circles of chromosomes indicating that two complexes are identical or similar while a circle of fourteen chromosomes signifies the greatest degree of dissimilarity between the two complexes. This suggested that chromosomal end arrangement might be useful as a measure of phylogenetic relationship and thus lead to an understanding of the evolutionary history of the group. The genus *Oenothera* had long been a problem for taxonomists because of the large number of intergrading forms that hybridize freely. Cytogenetic analysis showed promise for identifying phylogenetic groupings, which then might be a basis for a more satisfactory taxonomic treatment of the genus.

*J. Belling, "The Attachment of Chromosomes at the Reduction Division in Flowering Plants," *Journal of Genetics*, 18(1927):177–205.

† More commonly called reciprocal translocation.

A study of collections from natural populations throughout California initiated this new direction of Cleland's work, which was to become the main thrust of his research for the remainder of his career. Following study of the California races, the work expanded into a cytogenetic analysis of large numbers of *Oenothera* collections from throughout North America; the objective was to understand the genetic and chromosomal structure of natural populations and thereby trace their evolution.

In 1938 Cleland left Goucher College to assume the chairmanship of the Department of Botany at Indiana University. Here his research program on *Oenothera* population structure gained momentum with the support of the Rockefeller Foundation and with the aid of various research associates and graduate students.

The progress of these studies was reported in a series of papers beginning in 1940 with "Analysis of Wild American Races of *Oenothera* (*Onagra*)," in which the various phylogenetic groups were identified and described in a provisional way. The subsequent work by Cleland and his associates concentrated on the cytogenetic analysis of over 300 collections and led to a more precise characterization of the different groups and their evolution. These studies, which extended over nearly thirty years, were summarized and reviewed in Cleland's book, *Oenothera: Cytogenetics and Evolution,* completed shortly before his death.

While the main thrust of Cleland's research in the latter years took the direction of *Oenothera* population studies, he also published a number of papers on such more-or-less unrelated genetic topics in *Oenothera* as chromosome structure and behavior, incompatibility factors, and the inheritance of cruciate petals. A number of these studies were carried out during his retirement years. It is noteworthy that Cleland's scientific contributions extended over a period of fifty years.

His papers were consistently significant. As new problems arose, he attacked them with success, focusing on the significant and avoiding the trivial.

Cleland's distinction in research brought him national recognition and subsequent election to leadership positions in various professional scientific societies as well as numerous honors and awards. He served on many national committees dealing with scientific matters. In 1950 he assumed the deanship of the Graduate School of Indiana University, at the same time continuing as chairman of the Department of Botany. He held both positions until his retirement from administrative duties in 1958. Cleland was a member of the National Academy of Sciences, the American Philosophical Society, and the American Academy of Arts and Sciences. He served as president of the Genetics Society, The Botanical Society of America, the American Society of Naturalists, and the Indiana Academy of Science. Other honors included the first John F. Lewis Award of the American Philosophical Society and the Golden Jubilee Merit Citation of the Botanical Society. He was a corresponding member of the Deutsche Botanische Gesellschaft and an honorary member of the Genetics Society of Japan and the Botanical Society of Korea. Cleland held honorary degrees from Hanover College, the University of Pennsylvania, and Indiana University.

Cleland possessed an unusual combination of personal characteristics that undoubtedly played an important role in the professional achievement he attained. In some respects he seemed a shy man, yet he possessed a quiet self-assurance that enabled him to present his research conclusions effectively at a scientific meeting, even as a young scientist whose work was just getting under way. In the early years, when he undoubtedly carried a relatively heavy teaching load, he devoted his summers to research, and to growing, gathering, and preparing material for study throughout the academic year. His consistently significant research output was undoubtedly the result, not only of long hours, but of a persistence and steady application to the task at hand. Nevertheless, he was always available to his students; he never gave evidence of resentment or impatience at being interrupted. His calm, unruffled personality enabled him to shift from one activity to another with a minimal lag effect, using his time efficiently. In later years, because of his involvement in national scientific affairs, he traveled to Washington on a regular schedule and was often away from his laboratory as much as he was there. He arranged his teaching schedule to adapt to these demands, not infrequently returning to campus only moments before his lecture.

Cleland had a high regard for the academic way of life, and particularly for creative scholarship. The fact that his three sons all chose academic careers was a great satisfaction to him. He was a conscientious teacher who set high standards for his students. He willingly taught at the introductory as well as at the graduate level. Although not a charismatic speaker, he was nevertheless articulate, and his lectures were well organized, accurate, and up-to-date.

While many high achievers in science frequently have fragile egos requiring continuous nurture, Cleland obtained his satisfactions from an inner conviction that his contributions were significant and sound. He was essentially a modest person, readily approachable, lacking any trace of an exaggerated sense of self-importance. He was always willing to do a menial task when it was expedient. His concern and consideration for others were shown not only in his personal relationships but also in his support of programs that would contribute to the well-being of the community as a whole. He remained an active church member throughout his life. While on occasion his students may have considered him a bit straight-laced because of his opposition to smoking and alcohol, he nevertheless held their respect and admiration. Ralph and Elizabeth Cleland lived without ostentation. Their home radiated a warm and comfortable atmosphere. They both had a positive, optimistic, and cheerful attitude toward life with an enthusiastic involvement in the affairs of the University, the community, and the world as a whole. This persisted even after Mrs. Cleland became an invalid.

Cleland had a deep interest in music. For many years he was a regular member of a group that assembled in Alfred Kinsey's home to listen to music in a serious way. Whenever possible he attended the concerts and was proud of the quality of the musical offerings at Indiana University. It was thus highly appropriate that the memorial service following his death took the form of a concert.

After retiring from administrative posts at the age of sixty-five, Cleland returned to teaching until complete retirement at seventy. Subsequently he continued his research, pursuing various problems that earlier had lower priority in his research program. Ralph Cleland was the last survivor of the investigators who had played a major role in the unravelling of the *Oenothera* problem and who had had direct contact with most of the prominent workers in the field initiated by Hugo deVries. It was thus particularly important that he write a book reviewing the massive *Oenothera* literature and providing an up-to-date critical summary of the *Oenothera* work. In typical fashion, the project moved ahead on schedule and the manuscript was completed only a few days before he was stricken with a heart attack in his laboratory.

HONORS AND DISTINCTIONS

DEGREES

A.B., University of Pennsylvania, 1915; M.S., 1916; Ph.D., 1919
Sc.D. (honorary), Indiana University, 1970
Ll.D., Hanover College, 1957

ACADEMIC POSITIONS

Goucher College: Instructor of Biology (1919–1920); Assistant Professor (1920–1923); Associate Professor (1923–1930); Professor (1930–1938); Chairman of Department (1937–1938)
Indiana University: Professor and Chairman, Botany Department (1938–1958); Dean of Graduate School (1950–1958)
Instructor, University of Michigan, summer 1920
Instructor, Marine Biological Laboratory, summer 1925

EDITORIAL POSITIONS

Editor, *Plant Cytology, Biological Abstracts,* 1925–1972
Trustee, *Biological Abstracts,* 1943–1948
Editor-in-Chief, *American Journal of Botany,* 1940–1946
Editorial Board, *American Journal of Botany,* 1946–1953

AWARDS

Phi Beta Kappa
Sigma Xi
First John F. Lewis Award, American Philosophical Society, 1937
Golden Jubilee Merit Citation, Botanical Society of America, 1956
Guggenheim Fellowship, 1927–1928; Renewed, 1928

PROFESSIONAL AND HONORARY AFFILIATIONS

Fellow, American Association for the Advancement of Science (Council at various times; Vice-President and Chairman of Section G, 1944)
Fellow, Indiana Academy of Science (President, 1959)
Fellow, American Academy of Arts and Sciences
Member, Botanical Society of America (President, 1947)
Member, Genetics Society of America (Vice-President, 1955; President, 1956)
Member, American Society of Naturalists (Secretary, 1938–1940; President, 1942)

Member, Society for Study of Evolution
Member, International Society for Cell Biology
Member, American Philosophical Society
Member, National Academy of Sciences
Honorary Foreign Member, Genetics Society of Japan
Honorary Life Member, Botanical Society of Korea
Corresponding Member, Deutsche Botanische Gesellschaft
Organizing Committee, Member of Governing Board, and first Chairman (1948–1949), American Institute of Biological Sciences
Chairman, Division of Biology and Agriculture, National Research Council, 1948–1951
Chairman or Member of many NRC committees, including: UNESCO Committee; Maize Committee; Kimber Award Committee; Agricultural Board; NRC, NSF, and Fulbright Fellowship panels or boards; Pacific Science Board; Advisory Committee, Office of Scientific Personnel (Chairman); Advisory Committee, International Organizations and Programs, Office of Foreign Secretary
Member, Advisory Committee to Selective Service, 1951–1953
Member, U.S. National Commission for UNESCO, 1958–1960
Consultant, National Science Foundation, 1952–1959
Secretary-Treasurer, Association of Graduate Schools of the Association of American Universities, 1955–1958
Chairman, American Delegation to 7th International Botanical Congress, Stockholm, 1951
Member, American Delegation to 9th International Genetics Congress, Bellagio, 1953
Member, American Delegation to General Assembly, International Union of Biological Sciences (IUBS), Nice, 1953
Vice-President, IUBS, 1953–1959
President, Genetics Section, 8th International Botanical Congress, Paris, 1954
Sent with Farrington Daniels by the National Academy of Sciences to Southeast Asia as "Scientific Ambassador," 1960; visited thirteen countries during three-month trip. Also served as consultant for the Asia Foundation

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1919

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1922

The reduction division in the pollen mother cells of *Oenothera franciscana*. Am. J. Bot., 9:391–413.

1923

Chromosome arrangements during meiosis in certain oenotheras. Am. Nat., 57:562–66.

1924

Meiosis in pollen mother cells of *Oenothera franciscana sulfurea*. Bot. Gaz., 77:149–70.

1925

Chromosome behavior during meiosis in the pollen mother cells of certain oenotheras. Am. Nat., 59:475–79.

1926

Meiosis in the pollen mother cells of *Oenothera biennis* and *Oenothera biennis sulfurea*. Genetics, 11:127–62.

Cytological study of meiosis in anthers of *Oenothera muricata*. Bot. Gaz., 82:55–70.

1928

The genetics of *Oenothera* in relation to chromosome behavior, with special reference to certain hybrids. Z. Induk. Abstamm. Vererbungsl., Suppl. Bd., 1:554–67.

1929

Meiosis in the pollen mother cells of the oenotheras, and its probable bearing upon certain genetical problems. Proc. Int. Congr. Plant Sci., 1:317–31.

Chromosome behavior in the pollen mother cells of several strains of *Oenothera lamarckiana.* Z. Induk. Abstamm. Vererbungsl., 51: 126–45.

With F. Oehlkers. New evidence bearing upon the problem of the cytological basis for genetical peculiarities in the oenotheras. Am. Nat., 63:497–510.

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1930

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1931

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1933

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1934

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1935

Chromosome configurations in *Oenothera* (*grandiflora* x *lamarckiana*). Am. Nat., 69:466–68.

Cytotaxonomic studies on certain oenotheras from California. Proc. Am. Philos. Soc., 75:339–429.

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David M. Mottier. Science, 91:423–24.

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1942

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1950

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1972

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