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ROY ELWOOD CLAUSEN

1861—1956

A Biographical Memoir by
JAMES A. JENKINS

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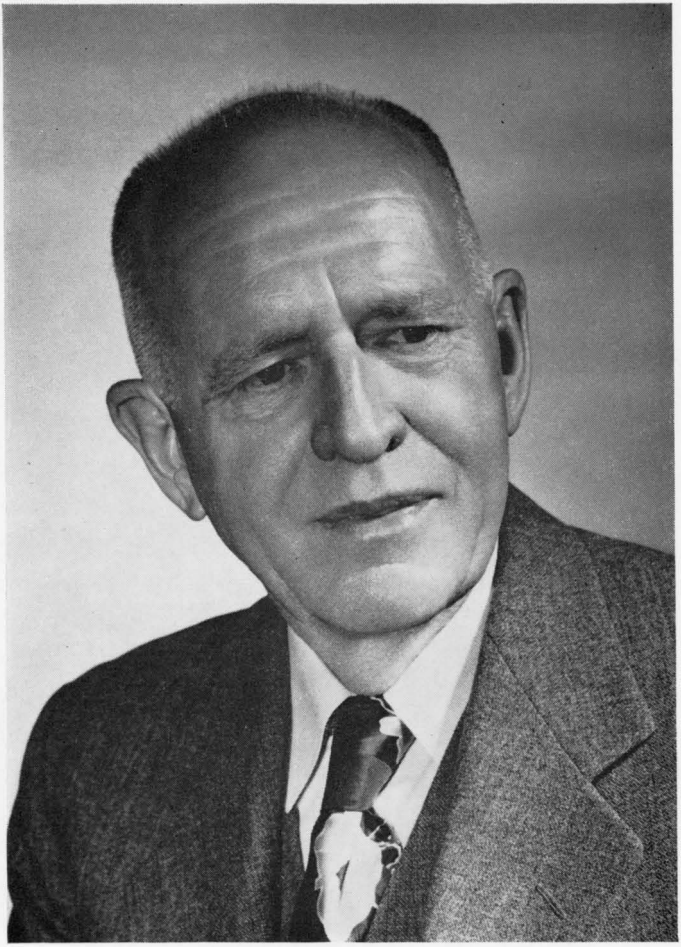

Roy D. Clausen

ROY ELWOOD CLAUSEN

August 21, 1891–August 21, 1956

BY JAMES A. JENKINS

ROY ELWOOD CLAUSEN was an uncommonly gifted man who was most admired by those privileged to know him well. He was widely recognized as the author of an impressive series of cytogenetic studies in the genus Nicotiana and as coauthor of a classic text, *Genetics in Relation to Agriculture.* To acquaintances he presented an exterior of quiet good humor; he did not intrude and was always willing to listen to those who had something to say. His reputation was highest, however, among students and colleagues—the better they knew him, the more they respected him. They respected him for his profound knowledge of genetics and above all for his thoughtful judgments in scientific and other matters.

His parents, Jens and Matilda Christianson Clausen, had come from Denmark as young children and had grown up on a farm near Randall, Iowa. Roy, the eldest of six children, was born on August 21, 1891, at Randall. He was a solitary child who spent much of his spare time reading. He began attending public school at Randall in 1897 and continued at Newkirk, Oklahoma, when his family moved there in 1900. On graduation from public school he immediately entered the University of Oklahoma at Stillwater as a subfreshman, and received the degree of Bachelor of Science in Agriculture in 1910. For his major in animal husbandry he completed a thesis, *A Study of Prizewinning Shorthorn Cattle, 1903 to 1909.* Aside from his major, his

special interest was mathematics. Upon graduation, rather than take over the family farm, he chose an academic career. Both he and his brother, Curtis Clausen, entered the University of California at Berkeley in 1910. He took a second bachelor's degree, graduating with honors in Agriculture in 1912 with a major in plant pathology. In 1914, at the age of twenty-two, he received his Ph.D. degree in biochemistry with a minor in plant pathology.

It is a measure of Clausen's promise as a student that a number of outstanding scientists went out of their way to encourage him. He was fortunate to meet William A. Setchell, Ernest B. Babcock, Thomas Hunt Morgan, A. Henry Sturtevant, and Calvin B. Bridges early in his career. They all became his friends and played a decisive role in shaping his future.

Soon after he arrived at Berkeley, Clausen came under the influence of the late William A. Setchell, an urbane scholar, who was then Chairman of the Botany Department. During his second year he served as Setchell's reader and on graduation became a research assistant for Setchell on the Nicotiana project. Although he took his Ph.D. degree in biochemistry, he continued as research assistant on the Nicotiana project. Setchell made a profound impression on Clausen; as the latter remarked later, "Setchell's interests, his insatiable curiosity and his boundless energy always fascinated me." Not only was this early association with Setchell the beginning of a long and intimate friendship, but it was also the beginning of Clausen's own investigations on Nicotiana, which were to remain the dominant research interest for the remainder of his life.

Because of his curiosity about the origin of tobacco and the spread of its uses, Setchell began assembling a living collection of Nicotiana varieties and species for the Botanical Garden in 1906. In attempting to untangle the nomenclature of the many seed lots he became convinced that the then current system of

varietal classification within the cultivated species *Nicotiana tabacum* was inadequate. What began as a simple taxonomic problem soon developed into a study of the origin of the hundreds of varieties within the cultivated species *N. tabacum.* In order to test current theory, Setchell chose five varieties that on morphological grounds he considered to be fundamental (primitive). He then attempted to select lines comparable to existing varieties from among the recombinations produced by hybridizing the fundamental varieties.

When Clausen joined the project as an assistant in 1912, Setchell and his student. Thomas Harper Goodspeed, who had just received his Ph.D. degree, were studying the first hybrid generation. From this point on, Setchell gradually withdrew from active participation in the investigations, and his two young protégés began nearly twenty years of a remarkably fruitful cooperation. Even as graduate students Goodspeed and Clausen found themelves well launched on productive research careers—the material was rich, the time was ripe, and they made the most of their opportunities. They applied the principles of Mendelian genetics to the varietal differences within *N. tabacum* in an attempt to unravel the evolutionary history of the cultivated species. Each experiment was to them an exciting new discovery, and many of their discoveries were new to genetics.

A second decisive influence in Clausen's career came in 1914 when Ernest B. Babcock invited him to join the newly formed Division of Genetics in the Department of Agriculture. Although Clausen had no formal training in genetics, he had a rich background of experience for this new assignment: animal breeding, mathematics, plant pathology, plant hybridization, and biochemistry. Without neglecting his Nicotiana investigations, he began to prepare himself to teach a course in genetics and to develop material for laboratory instruction and student research. Since

there was no satisfactory introductory text, Babcock and Clausen undertook to write one. Their *Genetics in Relation to Agriculture* first appeared in 1918, with a second edition in 1927. This text, especially the second edition, was a remarkable synthesis of genetic principles and their applications to plant and animal breeding. It was enthusiastically received both as an introductory text and as a reference book. Even today it is a valuable guide to the early literature on the chromosome theory of heredity.

Two years after becoming established in his new position, he had the good fortune to meet Thomas Hunt Morgan. Clausen had been collecting Drosophila mutants for class and student research and in the course of analyzing these mutants had corresponded with Morgan. In 1916 the latter gave a series of five Hitchcock lectures on the Berkeley campus under the general title "The Bearing of Modern Work in Genetics on the Theory of Evolution." Morgan, who had just published *The Mechanism of Mendelian Heredity* with Sturtevant, Muller, and Bridges, was at the time uniquely qualified to re-examine Darwinian concepts and to give a new impetus to evolutionary studies. Clausen found this association most stimulating.

After an eighteen-month absence in military service, spent largely at Camp Lewis, Washington, as supply officer in a depot brigade, Clausen resumed his Nicotiana and Drosophila investigations in the spring of 1919. His interest in the Drosophila mutants was greatly increased by an extended visit of T. H. Morgan, this time accompanied by his associates, C. B. Bridges and A. H. Sturtevant. They came fully equipped with Drosophila stocks to set up a laboratory on the Berkeley campus from June to September 1921. No more fitting climax to a young geneticist's education could be imagined than the give and take of discussion with this famous trio. Above all, Clausen cherished the close personal friendships that grew out of this visit—especially that with Sturtevant.

During this period Clausen resumed his analysis of the dihybrid Drosophila mutant ski-wings, which he had discovered in 1915. He also found four new mutants in natural populations: jaunty wings and cinnabar eyes in *Drosophila melanogaster* as well as white and vermilion eye-colors in the related species *D. hydei*. The results of his Drosophila studies were published in three papers, one in collaboration with J. L. Collins. Although he continued work with *D. hydei* for many years, the Nicotiana investigations took more and more of his time. Ultimately, he gave his Drosophila stocks to Warren P. Spencer, but unfortunately a large body of data remains unpublished.

It is remarkable that throughout his long career of more than forty years, Clausen's Nicotiana investigations were directed to the solution of a single problem: How did the very great genetic diversity within the cultivated species *N. tabacum* arise? True, it was an important and challenging problem central to the whole concept of evolution by natural selection and therefore worthy of a lifetime's devotion. But that he saw it as a fresh challenge for so long was characteristic. He was attracted by puzzles and had the capacity to mull them over for long periods until he saw a solution. Furthermore, he was never content with a plausible answer. He demanded consistent answers from as many independent lines of evidence as possible, and he had a sharp eye for inconsistencies.

It was also characteristic of Clausen that while collaborating with colleagues throughout his career, principally with Goodspeed and after 1934 with Donald R. Cameron, he was, paradoxically enough, a solitary worker. He seemed to enjoy even routine tasks of research and found relaxation in observing and hybridizing plants in the field.

Clausen's Nicotiana investigations can be divided into three periods on the basis of the method of analysis used. The first of

these, the Mendelian period, was just getting under way when Clausen joined the project in 1912. Although the analysis of progenies of hybrids between varieties within *N. tabacum* did not yield any novel genetic situations, it did give an indispensable background for further genetic analysis. A few clear-cut segregations, mostly of flower colors, provided marker genes that were of use in subsequent investigations. The most important conclusion, however, was that modifying genes obscured the segregation of many marker genes. Thus from the very beginning the value of a uniform genetic background was realized and all new genes were routinely transferred to a single inbred variety, *N. tabacum* var. *purpurea.* By this device it was much easier to detect new variants that differed only slightly from the "normal."

Apart from the few cases of clear-cut segregations, the genetic differences among varieties could be referred to a great many gene differences, each with a small effect. A few cases of size differences among varieties in flowers and leaves were reported in detail. But the central problem remained—the origin of these many gene differences—the more so as very few mutations had been observed under controlled conditions. Since no wild prototype of *N. tabacum* had been reported, it was assumed that the very great varietal diversity had occurred during the few thousand years of domestication.

Interspecific hybrids, on the other hand, showed an entirely different genetic behavior. In the *tabacum* × *sylvestris* hybrid, for example, there was a rapid return to the parental types within a few generations with relatively few recombinations of parental characters surviving. In 1916 Goodspeed and Clausen proposed the reaction system hypothesis to explain this wide departure from Mendelian expectations. They proposed that the elements (genes) of *tabacum* and *sylvestris* could not freely recombine because they belonged to different reaction systems.

This formal explanation was revised in 1926 to conform with Goodspeed's 1923 discovery that the first generation *tabacum* × *sylvestris* hybrid had 12 paired chromosomes and 12 unpaired chromosomes, which he interpreted as the result of the 12 *sylvestris* (12_{II}) × *tomentosa* (12_{II}) → F_1 *sylvestris-tomentosa* (24_I) chromosomes and leaving 12 *tabacum* chromosomes unpaired. At meiosis the unpaired chromosomes were distributed at random and only those gametes functioned that received either 12 or 24 chromosomes or numbers close to these extremes.

Goodspeed's 1923 preliminary note on the cytology of Nicotiana species and hybrids was the beginning of the second period in the Nicotiana investigations: the period of hybrid cytology. Chromosome pairing in hybrids proved to be a fruitful method for determining the relationships of the various species.

The discovery and investigation of the synthetic species *N. digluta* with 36 pairs of chromosomes threw unexpected light on the origin of species in Nicotiana. *N. digluta* appeared in 1922 through spontaneous doubling of the chromosome number in the sterile hybrid *glutinosa* (12_{II}) × *tabacum* (24_{II}). In the 72-chromosome amphidiploid, the 48 *tabacum* chromosomes could form 24 pairs and the 24 *glutinosa* chromosomes 12 pairs. *N. digluta* was crossed with both parents, yielding the following results:

digluta (36_{II}) × *glutinosa* (12_{II}) → F_1 *digluta-glutinosa* ($12_{II} + 24_I$)

digluta (36_{II}) × *tabacum* (24_{II}) → F_1 *digluta-tabacum* ($24_{II} + 12_I$)

Thus it was clear how *tabacum* and other 24-paired species could arise through doubling the chromosome number in a sterile hybrid between two 12-paired species. Furthermore, a cytological technique was available for recognizing putative parents of polyploid species in Nicotiana and other genera.

As applied to the analysis of *N. tabacum,* the following crossing data showed that the 24 pairs of *tabacum* chromosomes

consisted of two subsets of 12 chromosomes each: a *sylvestris* subset, homologous with those of *N. sylvestris,* and a *tomentosa* subset, homologous with those of *N. tomentosa.* In confirmation, through direct crossing the *sylvestris* and *tomentosa* chromosomes proved nonhomologous with each other:

sylvestris (12_{II}) $\times$ *tabacum* (24_{II}) $\rightarrow$ F_1 *sylvestris-tabacum* ($12_{II} + 12_I$)
tomentosa (12_{II}) $\times$ *tabacum* (24_{II}) $\rightarrow$
F_1 *tomentosa-tabacum* ($12_{II} + 12_I$)
sylvestris (12_{II}) $\times$ *tomentosa* (12_{II}) $\rightarrow$ F_1 *sylvestris-tomentosa* (24_I)

During 1938–1942 Clausen's student Greenleaf[1] succeeded in producing a number of amphidiploid Nicotiana that resembled *tabacum* by doubling the chromosomes of the following sterile hybrids: *sylvestris* $\times$ *tomentosa, sylvestris* $\times$ *tomentosiformis,* and *sylvestris* $\times$ *setchellii.* Like *tabacum* these synthetic amphidiploids had normal pollen meiosis with 24 pairs of chromosomes and produced normal pollen that was fully fertile when applied to *tabacum.* On the other hand, they were completely female sterile. Obtaining these synthetic *N. tabacum* made it abundantly clear that *tabacum* arose through chromosome doubling between *sylvestris* and some member of the *tomentosa* assemblage. There must, however, have been modifications in the course of evolution from the raw amphidiploid to the modern *tabacum* varieties. Elimination of female sterility was, of course, one obvious modification. Clausen was impressed by a less obvious one. If *tabacum* combined two self-sufficient chromosome sets, it should contain a great many duplicated genes. Yet there was relatively little evidence for duplicate genes. Clausen immediately saw that he could demonstrate the presence of duplicate genes if he had a complete set, that is, 24 distinct monosomics, each lacking a different chromosome. He therefore undertook to produce a complete set of *tabacum* monosomics and to carry out the analysis.

[1] Walter H. Greenleaf, *Journal of Genetics,* 43(1942):69-96.

The value of monosomics for genetic analysis grew out of cytological investigations of a number of anomalous plants that appeared in low frequency in cultures of *N. tabacum* var. *purpurea.* This variety had been self-fertilized from the beginning of the Nicotiana studies and was therefore exceedingly uniform genetically, which made it possible to detect and study minor departures from the standard that otherwise might pass unnoticed. Some anomalous types that did not transmit their characteristics in regular Mendelian fashion proved to have chromosome abnormalities. Cytological investigation of these anomalous plants gave Clausen and Goodspeed a deeper insight into the problem of the origin of *tabacum* and of its great varietal diversity. At the same time, analysis of anomalous lines served as a point of departure for Clausen's subsequent monosomic investigations and thus initiated the third and most fruitful period of Clausen's Nicotiana studies.

The first report of these anomalous plants dealt with two periclinal chimeras. In both cases only the outer layers showed the mutant flower color; the inner layers, from which the gametes were formed, were unaltered. Thus no genetic line was established from the mutant tissue. These two cases did, however, alert Clausen and Goodspeed to the behavior of chimeric plants and aided materially in their understanding of the carmine-coral variegation to be mentioned later.

The second anomaly was a haploid *tabacum* plant, the first of many, that, apart from its intrinsic cytological interest, provided evidence that the two sets of 12 chromosomes in *N. tabacum* were not sufficiently homologous to form pairs. As pointed out above, Clausen and Mann concluded in 1924 that in the *tabacum-sylvestris* hybrids the 12 pairs were made up of 12 *sylvestris* chromosomes and 12 *tabacum* chromosomes, leaving 12 *tabacum* chromosomes unpaired. A second haploid, reported together with his student Walter E. Lammerts (1929),

was unusual in that the chromosomes were derived from the male rather than the female gamete, as is usually the case.

The third anomaly, the trisomic enlarged with 49 rather than the 48 chromosomes characteristic of *tabacum*, was recognized because of its larger flowers. It transmitted the extra chromosome in about 36 percent of the female gametes and only in about 3 percent of the male gametes. The double trisomic with a pair of extra chromosomes was even more erratic in its transmission of extra chromosomes. In 1924 Clausen and Goodspeed demonstrated that it, or for that matter any other trisomic, did not lead to a permanent increase in chromosome number. While Clausen realized the value of trisomics for locating genes in a definite chromosome, he saw them principally as a means of determining the origin of individual chromosomes in *tabacum*. Almost immediately, however, he was attracted to the monosomics, which were even more valuable as a means of determining the origin of individual *tabacum* chromosomes.

In 1926 Clausen and Goodspeed reported on the first two monosomics: fluted (haplo F), which arose as a spontaneous mutant in *N. tabacum* var. *purpurea* cultures, and corrugated (haplo C), which arose in the progeny of *tabacum* × *sylvestris* backcrossed to *tabacum*. Presumably the latter monosomic was produced by the union of a 23-chromosome gamete from the hybrid and a normal 24-chromosome gamete from the *tabacum* parent. If so, the missing chromosome from the hybrid gamete probably belonged to the *tomentosa* subset, because there were two sets of *sylvestris* chromosomes, one from the *sylvestris* subset of *tabacum* and one from the *sylvestris* parent, which would be distributed regularly to all offspring. If this hypothesis was substantiated, Clausen saw a method for transferring individual chromosomes one at a time from both *sylvestris* and *tomentosa* to *tabacum*. Such an analysis required a complete set of 24

monosomics of normal *tabacum*. He immediately undertook this theoretically simple but nevertheless arduous task.

Clausen also carried out an extended study of fluted and its derivatives, coral and mammoth. Loss of a single F chromosome, presumably as a consequence of occasional nonconjugation, in *N. tabacum* var. *purpurea* produces the monosomic fluted. Both coral and mammoth, which appeared in the progeny of fluted, were shown to be secondary modifications by fragmentation of the F chromosome. The fragmented F chromosome in coral also gave rise to an unstable carmine-coral variegation when crossed to normal carmine-colored *purpurea*. This was subsequently shown to be the consequence of an unstable ring chromosome. The tendency of unpaired chromosomes to become modified in later generations was a complicating factor in producing the 24 primary monosomics and in maintaining them after they were produced.

After 1934 Clausen had the able cooperation of Dr. Donald R. Cameron and from time to time the assistance of several graduate students. The production of the 24 monosomics was also materially aided by the discovery of an asynaptic gene in *N. tabacum* var. *purpurea,* which made it unnecessary to hybridize *tabacum* with *tomentosa* and *sylvestris*. Nevertheless, the success of the whole program depended upon Clausen's sharp eye in recognizing deviating plants. He enjoyed the many hours that he had to spend in the tobacco field, hours which he looked upon as recreation. Furthermore, he communicated his enthusiasm and industry to his associates, some of whom became equally adept at recognizing deviating plants. By 1944 Clausen and Cameron had succeeded in isolating 24 different monosomics. Even with all of their precautions, however, they were not entirely certain that every monosomic was truly primary, that is, contained an unmodified chromosome.

Monosomic analysis was not entirely new: in essence it

consisted in extending the advantages of sex-linked inheritance to all the chromosomes of a species one at a time. By 1944 the monosomic chromosomes in each of the 24 lines could be assigned to either the *tomentosa* or the *sylvestris* subset. Ten genes had been located in four chromosomes of the *tomentosa* subset and eight genes in five chromosomes of the *sylvestris* subset. With this beginning it was possible to answer some of the evolutionary problems peculiar to such polyploid species. For example, if *N. tabacum* arose by doubling the chromosome number of a sterile hybrid between *sylvestris* and *tomentosa,* the raw amphidiploid must have contained many duplicate genes, yet the modern *N. tabacum* seems to have relatively few and moreover does not tolerate extensive deletion of chromosome material. Through monosomic analysis Clausen demonstrated that sheltered lethals do exist. That is, if one member of an originally duplicated pair of genes mutated to a lethal condition, the other would become a shelter gene. A relatively few such sheltered lethals well distributed would make *N. tabacum* behave essentially as a diploid species. On the other hand, what appeared to be simple recessive mutations often proved, when subjected to monosomic analysis, to depend on duplicate genes. Monosomic analysis was also useful in understanding the process of alien substitution, that is, the transfer of a gene or genes for a character, particularly for disease resistance, from an unrelated species. In short, monosomic analysis opened up a whole field in the genetics of polyploid species.

Clausen excelled as a teacher of advanced students. Throughout most of his career he taught a course in cytogenetics that was a masterly synthesis of the subject. Students were impressed with the skillful selection of material, the organization, and the clear presentation. He attracted a loyal body of students by recognizing the talented and encouraging them. He was never too busy to discuss a genetic problem with

anyone and the discussion was always illuminating. Frequently he puzzled over a problem for a long time and somehow induced the student to do likewise. In these cases, the resolution of the problem was most gratifying to the student because it was the result of a free interchange of ideas.

Through his long years of service on faculty and administrative committees, particularly the Committee on Budget and Interdepartmental Relations, he played a considerable role in directing the affairs of the University. His value in this area was compounded of his deep sense of loyalty to the University as well as his courage and integrity. Because he appeared outwardly calm and often jovial, few people realized the extent of his commitments or what they cost him. His many exacting duties, together with his services at the Los Alamos Scientific Laboratory during 1944 and 1945, adversely affected his health. Although he tried to avoid administrative and committee assignments on his return to the Berkeley campus, he was persuaded to serve as Chairman of the Department of Genetics, which he did until his death from a heart attack on August 21, 1956.

Because of his ability, Clausen held numerous offices in scientific societies, including that of President and Chairman of the Pacific Division of the American Society for the Advancement of Science (1947-1948), Secretary General of the Sixth Pacific Science Congress (1939), and President of the Genetics Society of America (1953). His election to membership in the National Academy of Sciences (1951) and his selection by fellow faculty members to the Faculty Research Lectureship (1954) were in just recognition of his contributions to science and scholarship.

Clausen married Mae Winifred Falls in 1916; she died in 1959. They are survived by their son Roy, a colonel in the Medical Corps, U.S. Army, and three grandchildren.

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KEY TO ABBREVIATIONS

Am. Naturalist = American Naturalist
Proc. Nat. Acad. Sci. = Proceedings of the National Academy of Sciences
Univ. California Publ. Bot. = University of California Publications in Botany

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