NATIONAL ACADEMY OF SCIENCES

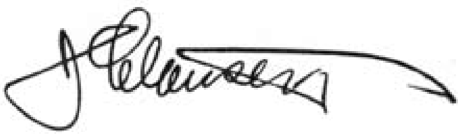
JENS CHRISTIAN CLAUSEN

1891—1969

A Biographical Memoir by
C. STACY FRENCH

Biographical Memoir

Carnegie Institution, Stanford, California



JENS CHRISTIAN CLAUSEN

March 11, 1891–November 22, 1969

BY C. STACY FRENCH

OBSERVERS OF NATURE—from primitive man to the most enlightened modern scientists—have long speculated on the relative importance of heredity versus environment in the development of living beings. With regard to humans the subject is so explosive that many fear to learn more. With regard to plants, however, the issue of development raises no controversy; experiments can be carried out in peace and results interpreted rationally. Working as the head of a plant biology research group at the Carnegie Institution, Jens Christian Clausen successfully clarified—for certain species and under certain conditions—the question of heredity versus environment so basic to biology.

When still a student in Denmark, Jens Clausen became interested in the genetics of a wide variety of local violet found near his home. A farm boy with sharp powers of observation, he had a mind that always asked why. His interest in living things eventually took him to Copenhagen University for his B.Sc. and M.Sc. degrees and, in 1926, the Ph.D. in the new field of genetics, and then to an assistant professorship at the Royal Agricultural College under Øjvind Winge—a scholarly botanist whom the young farmer-student held in considerable awe.

In the 1920s, while Clausen was making his name with his studies of Danish vegetation, Harvey Monroe Hall, professor of botany at the University of California, Berkeley, and a research associate of the Carnegie Institution, began transplanting native plants into contrasting environments. Supported by the institution, Hall and two student botanists, William M. Hiesey and David D. Keck, concentrated scattered transplants into three gardens with very different environments: one near sea level at Stanford University, one at an elevation of 4,500 feet at Mather on the western edge of Yosemite National Park, and one at 10,000 feet at Timberline in the High Sierra of Yosemite's far eastern edge. In 1932, Hall invited Clausen to join his group as a geneticist. But a few months after Clausen's arrival, Hall died, leaving Clausen to take over as the project's director.

Jens Clausen's vigor and enthusiasm enabled him to spend long hours in the field and made him a natural leader and delightful colleague. A devoted Christian, Jens's faith reinforced a naturally strong character and joy in life, never limiting his independence of thought. He introduced many a famous botanist to the California vegetation of the mountain stations, and many had the good fortune, after a strenuous day of fieldwork, to enjoy his warm hospitality at the Mather "Hog Ranch" cabin.

In 1959, at the request of one of his students, Jens wrote a brief autobiography, which—written in his own words—fortunately preserves for us something of his spirit:

CONFESSIONS AND OPINIONS OF AN ECOLOGIST OF SORTS

Personal Background

Unfortunately, I must confess to being born in 1891—in the latter part of the nineteenth century. After a younger brother died when he was five and I ten years of age, I became, essentially, an only child.

I cannot claim much formal schooling because I went through only two grades of a four-grade, every-other-day country grammar school in Denmark, attending the two upper grades of this school between the ages of eight and thirteen. The principal of the school, who was also the teacher of the two upper classes, had advised my father to spare me from attending the beginner's classes by not starting me in school until I was past eight. He remained a personal friend of mine as long as he lived, but I must confess that I put little effort into the class work. Instead I did considerable extracurricular reading.

The grade school was followed by one year in a private, local secondary school, where I was introduced to the fundamentals of English, German, world history, physical and natural sciences, and mathematics. At the age of fourteen I left school entirely and took up the farming of my parents' fifteen-acre place. My father had been a house-builder during my early boyhood, and as I took over the daily running of the family farm, he resumed his primary interest. Unlike him, I had no inclination toward the building trade but was highly interested in farming. As a consequence, I never attended formal high school (or gymnasium as it was called in Denmark), but at the age of twenty-two presented myself for the entrance examination to Copenhagen University—an affair lasting a full month—and was admitted. Half a year later I had my B.Sc. degree at the University.

As far as my early education, I was largely autodidactic. I learned to read at the age of four using the daily newspaper as a primer and asking my father the meaning of the words. Curiosity was a driving force, and my father, who himself had been a quick learner, was a sensible person. My mother had never gone to school but learned at home. Before I normally would have started to school, I had learned reading, writing, and basic arithmetic. These skills opened the world of books to me, and being brought up on a farm I also became familiar with all kinds of living things and with farm practices. At various times during the early years one learned the principles of physics and chemistry from everyday experiments and had fun constructing primitive microscopes and telescopes.

My first introduction to botany was given me at the age of nine by an uncle who owned my mother's 5-acre birthplace in a botanically interesting part of the country, sculptured by high moraines and watercourses. My uncle was a farm laborer on a neighboring larger farm, but he was highly intelligent, interested in botany, and had by himself learned to recognize most of the Danish wild plants. I spent short summer vacations there, and on weekends he took me along on hikes over hill and dale and through forests. These trips opened a new world to me.

During my early teens, I borrowed from the county library Eugenius Warming's recently published book, *Plantesamfund,* the Danish forerunner of his later, *Ecology of Plants,* and considerably more inspired than its English successor. I became deeply interested in this subject, and during my high school years I made a detailed study of the botanical communities within a 2,000-acre moor area near my home and wrote a kind of term paper on the subject as part of my botanical training.

I likewise studied geology during my teens on small private expeditions around the country and on a trip to the famous Kinnekulle region in central Sweden, which contained a complete succession of the Cambrian and Silurian deposits. I returned from such expeditions with considerable paleontological and botanical loot. My home was also near primitive sites of middle stone age kitchen middens, and near remnants of a neolithic lake-dweller's community where stone axes of great artistic beauty had been manufactured for trade some 4,000 years ago. The hills were studded with burial sites from bronze and early iron age, uniting the past with the present.

News of the rediscovery of Mendelism drifted through the local newspapers, and in high school I also bought the sixth edition (1906) of Darwin's, *The Origin of Species,* in English. Receiving some private tutoring from Mr. Thorgiles, an unusual teacher who had become headmaster of the secondary school I once attended, I was now able to expand on my previous introduction to the sciences, mathematics, and the history of the civilizations of the world. Mr. Thorgiles, more than anyone else, was responsible for introducing me to the scientific method. A new grasp of foreign languages also opened German and English literature to me.

Therefore, although I did not attend formal high school, I probably had better training, going on my own, with a little guidance here and there. Life during those later teens was interesting and absorbing, as I managed a small dairy farm, pursued liberal studies of many kinds, and was church organist and church school teacher on the side.

My original plan had been to go to the Royal Agricultural College in Copenhagen as a preparation for a farming profession. From 1910, however, at the age of about nineteen, I was also a part-time teacher at the secondary school I had attended a few years earlier, teaching primarily science. This experience was absorbing, and I decided to change plans and attend the university instead. Starting at Copenhagen University in 1913 at the age of twenty-two, I majored in botany and minored in physics, chemistry, geology, geography, and zoology. In 1920, at the age of thirty, I received my master's degree in natural history and geography. During my student days, I continued to teach in the school but gradually tapered off on farming. I commuted the 30 miles to Copenhagen certain days of the week for the mandatory laboratory courses and some lectures. Two years—1916 to 1918—were spent in military service during World War I. At that time, stationed only 8 miles from Copenhagen, I commuted by bicycle.

The University of Copenhagen was a true university rather than a school. It did not have residence requirements and one more or less developed one's own plans for study in consultation with the professors. There were excellent opportunities for discussions with professors and with other students. Chresten Raunkiaer was my major professor in botany, P. Boysen Jensen in plant physiology, and Wilhelm Johannsen in plant physiology and genetics. I knew Eugenius Warming, who at that time was retired but still highly interested in the young students. August Krogh was my professor of animal physiology. I started physics under Niels Bohr, followed by H. M. Hansen, chemistry under Einar Biilmann and Chr. Winther, and geography under H. P. Steensby.

Intellectually, it was a highly stimulating environment. We were a small group of graduate students in biology who met for discussions, developing foundations for new approaches to systematics and ecology, sparked by the young science of genetics. In 1917 Winge defended his doctoral thesis on the significance of the numbers of chromosomes in plants, in which he proposed the polyploidy theory.

When I had my first interview with Wilhelm Johannsen in 1913, I mentioned that, for my master's degree, I wanted to choose a specialty in genetics, and that I was interested in combining the genetic with the ecological approach to the study of systematics. Johannsen had no use for ecology and was rather amused at the suggestion. Genetics was still new at the time, and although Johannsen was one of its pioneers, nobody had ever before specialized in genetics. It was finally arranged that I should have a specialty both in systematics and genetics. At Raunkiaer's suggestion I chose the *Violaceae* because they were supposed to contain many natural hybrids.

Just at the time when Winge developed the polyploidy theories, I found that *Viola tricolor* had thirteen and *V. arvensis* (a close relative) seventeen pairs of chromosomes—not a polyploid situation. Moreover the two species hybridized at their points of contact in the wild, and the hybrids were moderately fertile. It so happened that spontaneous hybrid colonies of these two species of violet were located a short distance from the headquarters of the artillery company to which I was assigned, and I set up my microscope on the office desk of the company command. This was undoubtedly one of the queerest cannons in artillery history!

After the war I toured Denmark studying the wild populations of these two *Viola* species. I found prostrate, perennial races of *Viola tricolor* on exposed maritime sand dunes and annual, erect races inland—although often in close proximity to the maritime ones. Seedlings of the two kinds retained their identities even when grown remote from the coast. *Viola arvensis* was found to be associated with calcareous soils, *tricolor* with sandy soils. On neutral to faintly acid soils in the contact zones could be found swarms of interspecific hybrids, having intermediate, irregular chromosome numbers. Such spontaneous hybrids of various generations segregated similarly to the artificial hybrids. I presented these findings in two papers published in 1921 and 1922 in *Botanisk Tidsskrift.* They constitute one of the early approaches to experimental taxonomy, to studies on natural populations, and to the subject of gene introgression. These studies showed that the characters of the two species recombined at their points of contact, and that genes apparently could migrate some distance from the point of contact.

Remarkably enough, Göte Turesson's first papers on ecotypes appeared in 1922, and we discovered that, unknown to each other, we had been working on the same subject of races of species adjusted to ecologically distinct environments at sister universities only 30 miles apart, though in different countries. From that time on, there was fairly close liaison between Copenhagen and Lund across the sound.

At the Royal Agricultural College, Copenhagen, 1921–1931

After my master's degree, I started preparing for my teacher's credentials, although I had already taught for ten years. Three months later, however, in April 1921, the first genetics department in Denmark was established at the Royal Agricultural College. Øjvind Winge became professor, and I was offered the assistantship (corresponding to the rank of assistant professor). As a result I did not complete my teacher's credentials but landed unexpectedly at the college I originally had aimed for.

The field of the new department was to be basic research in genetics and not plant breeding—a far-sighted arrangement in an agricultural college. During the following ten years, the genic compositions of many kinds of plants and of the tropical freshwater fish, *Lebistes reticulatus,* were analyzed; the existence of sex chromosomes in several dioecious plant species was discovered; it was found that experimentally induced cancers of sugar beets and mice had abnormal chromosome numbers. We also studied interspecific hybrid progenies of several groups of plants of the genera *Melandrium, Geum, Tragopogon, Erophila,* and *Hypericum.* The papers relating these results are in Winge's name and much has never been published, but it was an excellent experience to work with so many different kinds of organisms.

On my own time, during evenings and vacations, I continued the investigations of the violet species of the Melanium section. These experiments resulted in a series of papers that were published in *Hereditas* between 1923 and 1931, and two papers on chromosome numbers and relationships of species published in *Annals of Botany* between 1927 and 1929. Mrs.

Clausen, although herself not a trained biologist, was a dedicated and skillful helper in the delicate and time-consuming work of crossing, pollinating, and classifying the large F_2 progenies, and of fixing and embedding the buds for cytological investigations.

My doctoral thesis, "Genetical and Cytological Investigations on *Viola tricolor* L. and *V. arvensis* Murr.," was published in *Hereditas* in 1926. As far as I know, this is the first demonstration of the fact that taxonomic characters distinguishing species are controlled by genes that can be analyzed. In Denmark, as in other Scandinavian countries, the doctorate is based on advanced research, the investigations are conducted after one has ceased being a student at the university, and there are no faculty advisors. The doctorate carries with it the right to lecture at the university on subjects of one's own choosing and to conduct courses there.

In 1927, I was granted a Rockefeller fellowship for one year at the University of California at Berkeley. In 1929, together with E. B. Babcock, who became a lifelong, close friend, I published a paper on chromosome pairing in three interspecific hybrids of *Crepis*. But the highly varied and diversified California vegetation, which I saw in the company of Babcock and others, had an even greater impact on my ecological thinking. In 1931, after my return to Copenhagen, I published a paper on chromosome pairing in C. H. Ostenfield's interspecific *Polemonium* hybrids.

With the Carnegie Institution of Washington at Stanford, 1931

H. M. Hall pioneered the transplant investigations in the Sierra Nevada beginning about 1921, and in 1923 cooperated with Babcock on a combined genetic-taxonomic investigation on the hayfield tarweeds, the Euhemizonia section of the genus *Hemizonia* of the Madiinae. Hall wrote me already in 1922 after my first two papers had been published that he was interested in conducting similar studies in California on plant relationships. We followed each other's work during the years and met both in California in 1927, and in Denmark in 1928. In 1930 I was unexpectedly offered a position as cytologist (later biologist) in his new program on experimental taxonomy, after the department of plant biology of the Carnegie Institution was established at Stanford in addition to the earlier stations in the Sierra Nevada. I accepted this offer in 1931 and arrived at Stanford in late October.

Tragically, Hall died four months later in Washington, D.C.—a great loss. I found myself unexpectedly chosen to take his place. It was fortunate for the future program that David D. Keck and William M. Hiesey, who had assisted Hall and knew the background of the plants were able to remain as part of the staff. Now began an interesting time of cooperation between men of quite different backgrounds and leanings, representing cytogenetics, ecology, taxonomy, and physiology.

Ecotype and Varied Environment Studies

Hall's transplant investigations, using plants of many genera and families that were cloned and grown in highly contrasting environments had been started to check on claims by Gaston Bonnier and F. E. Clements that lowland plants changed into alpines upon being transplanted, and vice versa. In analyzing the results of experiments under careful and constant control (published in 1940), it became obvious that no such change takes place, although the transplanted ramets are modified in their new environment.

It was more significant, however, that species widely distributed in western North America contain a fairly large number of physiologically distinct ecotypes, more so than Turesson observed in his extensive investigations in northern Europe. The most intensive sampling of natural populations came from a transect along the 38th latitude in central California, where two coast ranges parallel the coast and block the oceanic influence from the valleys. Beyond the Central Valley of California, the Sierra Nevada range paralleling the coast rises to 14,000 feet, removing the last of the oceanic influences so that the intermountain region is a desert plateau. This arrangement contrasts with the topographic situation in Europe, where the high mountains are at right angles to the coast and where the Atlantic influence is felt hundreds of miles from the coast. There are, therefore, fewer ecological zones in Europe than in California, and this is reflected in the ecotypic differentiation. A detailed analysis of natural populations and ecotypes in the *Achilles millefolium* complex was presented in a Carnegie Institution publication in 1948.

Evolution of Genetic Barriers

California species of the Madiinae of the Compositae were used in an investigation on populations and on ecotypic, interspecific, and intergenic differentiation. The species of the Madiinae are primarily diploid and have diploid chromosome numbers. More than 300 hybridization experiments have been conducted in this group of approximately eighty-five species of ten genera. The hybrids combined evolutionary entities that range over a scale from distinct ecotypes, over closely related species, to distinct taxonomic sections and genera.

As the data were assembled, it became obvious that they reflected a graded series of evolutionary separations. Morphologically distinct varieties of the same ecotype have simple genetic differences. Distinct ecotypes or subspecies of the same species are distinguished by complex gene systems, but their genes are still completely interchangeable. Farther along the scale, moderate genetic incompatibilities were encountered that resulted in weakness of the second generation and partial sterility in the first generation. In more effectively separated entities the genomes had become so differentiated that chromosomal pairing was almost eliminated in their hybrids. Even farther along, the entities were so different that they were unable to intercross, or if they crossed, the first-generation hybrid was sublethal. The details of most of these experiments are still unpublished.

Stages in the Evolution of Species

As the massed data of our own crossings were compared among themselves and with other data previously recorded in the literature, it became obvious that the evolutionary barriers to the interchange of heredities evolve gradually. There was a strong coincidence of strong barriers among species that good taxonomists had placed in distinct sections of a genus, while weaker barriers existed among closely related species of one section, the so-called ecospecies. Ecospecies tend to occupy ecologically distinct habitats, whereas remotely related species of distinct sections can occur together in the same habitat. The major lines of this development were sketched in the 1951 publication *Stages in the Evolution of Species.*

We found that evolutionary differentiation proceeds gradually from the stage of the local population to distinct ecotypes that occupy ecologically distinct zones, and to distinct ecospecies after partial barriers have evolved that prevent free gene exchange between certain of the ecotypes of the species complex. The differentiation proceeds to distinct cenospecies (species complexes whose genomes have become so different that chromosomal pairing is prevented in their hybrids but amphiploidy is still possible) and to distinct genera that are unable to intercross. Evolution is therefore reticulate until the level of the genus. From there on it becomes furcate, as Darwin represented it. The branches of the evolutionary tree are composed of genera, not of species, for the species form an evolutionary network within the branches. (See the 1945 Carnegie Institution publication for a report of this work.)

Apomixis

A very extensive series of experiments on the evolutionary aspects of apomixis, centering around the *Poa* genus, are in their concluding stages. Even to a greater extent than amphiploidy, apomixis can lead to rejuvenation of the genus, because it enables interspecific hybrids to escape some of the grueling interspecific gene interchanges. At the evolutionary stage of apomictic reproduction, the inheritance is no longer transferred as individual genes but as huge complexes of chromosomal complements, so that, quite often, entire genomes are being added, subtracted, or exchanged. Ecologically, the apomictic interspecific hybrids are especially important because genomes with their built-in ecologic adjustments can be transferred almost whole.

Apomictic seed clones also make it possible to undertake clonal transplant experiments on a worldwide scale because the clones can be established from seed rather than from ramets of live plants. Drs. Nobs and Hiesey cooperated with me on the *Poa* project, but it will require a couple of years to complete the detailed analysis of the responses of hybrid clones in many environments, to be followed by a written report.[1]

[1] The work was completed by Hiesey and Nobs and published in 1982 by the Carnegie Institution of Washington, Washington, D.C., under the title: *Experimental Studies on the Nature of Species. VI. Interspecific Hybrid Derivatives Between Facultatively Apomictic Species of Blue Grasses and Their Responses to Contrasting Environments.*

Genetic Structure of Ecological Races

The most important step in evolutionary differentiation is the rise of distinct ecotypes. Although it is possible that some agro-ecotypes may arise within a few centuries, most of our naturally occurring ecotypes have been in position in slowly changing environments, probably for millions of years. Such has been the case with coastal and alpine ecotypes of *Potentilla glandulosa,* belonging to the worldwide diploid species complex of the section Drymocallis. The species of this section are slowly developing, long-lived plants, and although they are semiwoody perennials, they can be cloned.

Individuals of lowland and alpine ecotypes of *Potentilla glandulosa* were intercrossed twenty-five years ago for the purpose of studying the kind of genic mechanism that distinguishes contrasting ecotypes of such a diploid and probably relatively primitive species of the genus. A second-generation progeny was cloned and was studied over many years in the contrasting environments of the lowland and mountain stations of the Carnegie Institution in central California. The responses of the ramets were recorded over successive periods of years.

This experiment, based on the combination of the genetic with the transplant method, revealed many new facts on the hereditary structure of related ecotypes and on the nature of the gene systems that distinguish such ecotypes. It opened the door to several highly neglected fields, such as the genetic structure of the elementary evolutionary entities, the range of phenotype expression of the same genotype in contrasting environments, and the interrelation among genes, processes, morphological expression, and environment. (The data are presented in a 1958 Carnegie Institution publication.)

Balance Between Variation and Coherence

There has been considerable speculation as to how neighboring ecotypes can remain relatively distinct. In the F_2 segregations of hybrids between ecotypes, it has now been shown that linkage exists between a sufficient number of the genes that control the parental characters so that the parental combinations are favored. Continued natural selection at the same time tends to favor the established ecotypes. Each of the characteristics of the ecotypes are regulated by several genes located in different chromosomes, and only some of the genes that regulate two characters are linked. Such a system causes moderate genetic coherence among characteristics of existing ecotypes as long as the environments remain relatively unchanged.

On the other hand, the ecotypes of a species store a great deal of unused or inactive variability that can become released after crossing; accordingly, the F_2s of interecotypic hybrids show considerable transgressive segregation. Normally, the selection will favor the parental combinations, but in times of geologic change a great deal of the genetic variation that is stored within the existing ecotypes can become released, and new gene combinations evolve fairly quickly from recombinations among hitherto unexpressed genes of existing ecotypes.

Many of the stored genes have been repressed by inhibitors; others are inactive because their complementary genes are found in another ecotype. The mechanism of linkage, which favors the retention of present combinations as long as conditions remain the same, will also accelerate the stabilization of new combinations after crossovers have occurred and a new kind of selective pressure has started.

Each characteristic is regulated by multiple genes, some of which have opposite effects, but only one or two of the genes that regulate a couple of characteristics are involved in the linkage mechanism, whereas the remaining genes can be linked with genes controlling other characteristics. This kind of genetic structure, in which potential variability is in balance with coherence mechanisms, provides a remarkable resiliency in ecotypes and in closely related ecospecies.

Evolution of Communities

The organisms of a community must, in their later stages, have evolved together, because they have achieved adjustment not only to the same kind of environment but also to each other. The organisms that exist in the same community are usually evolutionally remotely related. In contrast, phylogenetically closely related organisms (such as ecotypes and ecospecies of the same species complex) occur in ecologically distinct although often contiguous habitats. Moderate gene migration is possible between contiguous ecotypes and ecospecies, but genetic coherence and natural selection tend to keep them distinct.

The Search for the Differentiating Processes

Recently, the work of the experimental taxonomy group of the Carnegie Institution has entered a new phase by adding physiological laboratory research to the transplant and genetic method. This approach is now followed by Drs. Hiesey, Milner, and Nobs.

An unusually well-adapted organism has been found, the *Mimulus cardinalis-lewisii* complex. Along the central California transect, this complex has ecotypes ranging from an outer Coast Range lowland race to an alpine race at 10,500 feet altitude in the Sierra Nevada. *M. cardinalis* ranges from sea level to about 5,000 feet and is adjusted to pollination by hummingbirds, whereas *M. lewisii* goes from 5,000 to 10,500 feet altitude and is adjusted to pollination by bumblebees.

Morphologically, the two *Mimulus* species are so different that some taxonomists have placed them in distinct sections. Both are diploid, having eight pairs of chromosomes. They are easily hybridized by artificial pollination, the hybrids are fully fertile, and the second and later generations are vigorous. The parents and hybrids are self-compatible, but it is necessary to pollinate them artificially because the floral structures in the hybrid are such that none of the natural pollinators succeed. The two species are perennial but can be grown to maturity in one year. They can be cloned to an infinite degree because pieces of the stems can be rooted and develop to highly uniform new plants. The two forms have excellent morphological markers, and each has several ecological races.

Drs. Hiesey and Milner have developed an instrumentarium for the measurement of the photosynthesis-respiration ratios of cloned ramets over a wide range of accurately controlled laboratory conditions. The responses of the same parental and hybrid clones at the transplant stations will also be known and can be related to the laboratory findings. Controlled growth cabinets are also being developed so that the ramets can be accurately preconditioned before they are subjected to the metabolic tests. The methodology of these approaches is still being developed, but eventually these investigations will add another dimension to the experimental taxonomy investigations.[2]

The Future of Ecology

You asked for my opinion about the future of ecology. In the preceding sketch of the latest venture at our laboratory,

[2] The report of this work was published by William M. Hiesey, Malcolm A. Nobs, and Olle Björkman in 1971 as Carnegie Institution of Washington Publication no. 628 entitled: *Experimental Studies on the Nature of Species. V. Biosystematics, Genetics, and Physiological Ecology of the Erythrante Section of* Mimulus.

you have a part of the answer. This, however, is probably not what you had in mind.

Ecology as a separate discipline and wrapped up in its own mushrooming vocabulary, I feel, is on its way out, but so is any branch of science that is sufficient to itself and refuses cross-fertilization by other sciences. I am for biology of the inclusive kind that runs from cytogenetics over physics and chemistry, to the physiological and morphological expressions of the genotype in relation to the environment, culminating in a study of the evolutionary adjustment to environment. In my own lifetime I must be satisfied with a sense of the causal coherence among these processes. If, however, your definition of ecology implies such a chain of interacting processes, then it has a great future, and it will probably take a few centuries before we will be able in detail to trace some of the simpler chains of interaction.

Depending upon your own preference, you can name this branch of science evolution of living things, experimental taxonomy, biosystematics, genecology, etc., but it is the life sciences of the future. This kind of biology goes far beyond the narrow kind that the medically inclined fraction of our scientific fraternity carves out for itself and for which it has appropriated the fair name of biology.

I hope that these confessions, effusions, and opinions of mine have not been too lengthy or have sickened you on a sensible ecology. As you may have sensed from my background, I have a great love for an all-inclusive kind of ecology, and I consider it an honor when people introduce me as an ecologist, or, for that matter, as a geneticist, a botanist, or an evolutionist, because to me these are all-inclusive terms.

I am acutely aware that, irrespective of how one may extend the analysis of the forces and processes that regulate living things, we have obviously just barely touched the surface of this marvelously intricate and nevertheless highly coordinated mechanism we call a living plant. I suppose I was born with an innate curiosity concerning the world I am a part of myself. In the great drama of an evolving and changing world, the individual person and one's own lifetime seem of small significance, but the realization of this fact is more in the nature of a challenge than a discouragement. Learning to understand our world is a never-ending occupation.

JENS CLAUSEN
February 27, 1959

The above account in his own words takes us only to 1959, yet Jens's career continued with vigor and originality for ten more years, filled with discoveries and well-deserved honors. The institution's policy at that time of long-term support at a frugal level allowed the experimental taxonomy group (Clausen, Keck, Hiesey, and Nobs) to achieve a unique record in botanical research for continued progress on fundamental questions of plant relationships and evolution.

A man of great enthusiasm in proposing plans for elaborate experiments, Jens was also a stimulating leader and innovative interpreter of experimental results. In addition, his team benefitted from the careful deliberation and organizational ability of Hiesey, Keck, and Nobs in crystallizing significant conclusions.

During the war years Clausen became interested in the possibility of using apomixis in the evaluation of range grass strains to select those of superior quality. About two-fifths of the United States is used for cattle grazing; thus, any information that might lead to increased growth of range grass seemed likely to be of practical value. His thought was that crossing apomictic strains of grasses originating from contrasting environments that were unlikely to have crossed in the past might produce variations with new, and possibly favorable, mixtures of their characteristics. The pursuit of the *Poa* work for many years led to an increased understanding of plant evolution. No super range grass strains were developed as Clausen had hoped, however, in spite of a very large-scale effort and cooperation with many collaborators in Europe and the United States.

Some of the major contributions of Clausen's group were a thorough basic study of various kinds of ecotypes and their genetic structures, analysis of the composition and evolution of native species occurring across contrasting climates in a transect across central California, and an exploration of the possibilities and the limitations of crossing facultatively apomictic species of grasses and their responses when grown in different climates.

The clear establishment of "climatic races," which are adapted by heredity to growth in specific environments, finally demolished the Lamarkian idea that the modifications in growth form induced by changes in environment could influence a plant's genetic constitution. Thus, the controversy between E. F. Clements and H. M. Hall, which had been the principal reason for the transplant studies, was resolved. Furthermore, the linkage of inherited characteristics in specific groups was made evident by diagrams illustrating the way these groups of characters were distributed in the progeny of selected crosses. It became evident that the evolution of climatic races within an interfertile population takes place by exchanges of groups of linked groups of genes rather than by the slow accumulation of single gene mutations. These experiments required years of observations over many generations of plants with large numbers of samples. Such work cannot be done under a system of annual grants with questionable stability, nor can it be pursued effectively by investigators anxious for frequent promotions.

Evolutionary cytogenetics was a young science when Clausen took it up, but his work became a classic example of its possibilities. The results of his investigations and his noncompetitive joy in doing the work and in collaborating with colleagues and students have had a lasting effect on both the subject matter and on the investigators of plant life.

HONORS AND DISTINCTIONS

1949 Mary Soper Pope Medal of Botany, Cranbrook Institute of Science
1956 Certificate of Merit, Botanical Society of America
1956 President, Society for the Study of Evolution
1959 Member, National Academy of Sciences
1959 Royal Danish Academy of Science and Letters
1959 Fellow, California Academy of Science; American Association for the Advancement of Science
1961 Named Knight of Danneborg by King Frederick IX of Denmark
1961 Honorary Fellow, Botanical Society of Edinburgh
1961 American Academy of Arts and Sciences
1961 Royal Swedish Academy of Science

CHRONOLOGY

1891	Born March 11 in Eskilstrup, Denmark, 30 miles from Copenhagen, to Christen Agustinus Clausen and Christine Christensen
1905–1915	Farmer
1913	Entered Copenhagen University
1910–1916	Teacher in Danish secondary schools
1916–1918	Artillery Corps, Danish Army
1918–1920	Teacher in Danish secondary schools
1921	Married Anna Hansen (died Palo Alto, California, August 24, 1956)
1921–1931	Research Assistant, Department of Genetics, Royal Agricultural and Veterinary College, Copenhagen
1926	Ph.D., Copenhagen University
1927–1928	Research Fellow, International Education Board at the University of California, Berkeley
1931–1956	Staff, Department of Plant Biology, Carnegie Institution of Washington, Stanford, California
1936	Lecturer, University of Copenhagen
1943	Naturalized U.S. citizen
1950	Messenger Lectures, Cornell University
1950–1961	Trustee, Berkeley Baptist Divinity School
1951	Professor by Courtesy, Stanford University
1953	Lecturer in Brazilian universities
1956	Retired from Carnegie Institution of Washington (Jens preferred the word "pensioned" and kept on working all his life.)
1962	Lecturer, Vanderbilt University
1963	Lecturer, University of Chicago and Washington State University
1963–1964	Visiting Professor of Genetics, University of California, Davis
1966	Attended 11th Pacific Science Congress in Tokyo
1969	Died in Palo Alto, California, November 22

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