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MARINE BIOTECHNOLOGY

In Appreciation of Klaus D. Kallman

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To be exactly the right person in the right place at the right time does not often happen. When being the right person means having the potential to become one of the world's greatest fish geneticists, the probability of this happening drops close to zero. However, hindsight makes even minuscule possibilities look good. Adjunct Professor Myron Gordon of the Graduate School of Arts and Science of New York University certainly did not have such prescience when, in 1953, he first met Klaus D. Kallman, a new graduate student looking for a sponsor to direct his doctoral studies. Kallman had led a serious life. He was born in Berlin in 1928 and grew up there throughout the war and into the Russian occupation. He and his family eventually emigrated to the United States, where he continued his education at Queens College and received his B.S. degree in 1952. He had developed a keen interest in genetics as a teenager in Germany and had heard about Dr. Gordon's laboratory. When he saw the different platyfishes and swordtails attractively disporting themselves, he gladly accepted Gordon's offer to sponsor him. In less than a year, using a strain of platyfish Gordon had inbred for 16 generations of brother-to-sister matings, making them as genetically alike as identical twins, Kallman was able to begin his pioneering experiments on the immune system of fish. In 1955 he was awarded his M.S. degree and in 1959 his Ph.D. Dr. Kallman also received an honorary Ph.D. from the University of Hamburg in 1992.

Kallman's experiments indicated that a fish's immune system accepts or rejects transplanted tissue in a way similar to that of the well-known mammalian model, the laboratory mouse. It was up to him to develop a transplantation technique that worked with small fish. Each experimental animal had to be treated in precisely the same way to avoid uncontrolled variations.

Moreover, Kallman was planning to make thousands of transplants; therefore, he practiced transplanting fins and other organs from one small fish to another until it took him less than 1 minute to complete each operation. For more than a decade after publishing his doctoral thesis, Kallman used his hard-won technique to demonstrate the existence of individual parthenogenetic fish, to study self-fertilizing and gynogenetic species, to utilize the latter in experiments with organ transplants, and to analyze the genetic structure of natural fish populations (Kallman, 1970). Kallman had met his first major scientific problem and had satisfactorily mastered it.

Meanwhile, Kallman was becoming familiar with the complex operations of Gordon's meticulous genetics laboratory, particularly the record system of 3-by-5 cards that tracked the complete pedigree of each fish along with its color pattern, birth, matings, and the final disposition of its body. Furthermore, more than 600 aquaria had to be accounted for, each duly labeled with its inhabitants. Genetic experiments usually involve several generations spanning

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Professor Klaus D. Kallman, Director of the *Xiphophorus* Genetic Stock Center. This photograph was taken at the Osborn Laboratories of Marine Research, New York Aquarium, Brooklyn, New York, sometime in the late 1970s. (*Reproduced with permission from the Wildlife Conservation Society.*)

several years; dozens of experiments take place simultaneously, often involving hundreds of fish. Kallman never became overwhelmed by this orderly mass of extremely complicated, interrelated information. His complete familiarity stood him in good stead when, in April 1959, Gordon suddenly died. Less than a year later, Kallman was put in charge of the laboratory, which continued to function with little noticeable change. Unquestionably, Kallman knew more about what was going on in the New York Zoological Society's fish genetics laboratory than did anyone else. He had become "the man of the moment," and he continued to lead this premier laboratory for the next 33 years.

While overseeing all the laboratory's daily operations, including shipping live fish to investigators in other institutions, Kallman carried on his own vigorous research program. In all, he published at least 70 substantive papers, amounting to 1164 pages. A dozen of his articles concerned the unique sex chromosomes of the platyfish (*Xiphophorus maculatus*), which has 3 kinds instead of the usual 2: XY and YY males, and XX, WX, and WY females. The WW female has not been found in the wild, but was produced in the laboratory. In a most impressive review, Kallman (1984) marshals the evidence for a theory of how this system of sex differentiation evolved and argues convincingly against the idea that it simply results from the primitiveness of piscine chromosomes. However, the existence of atypical sex determination complicates the matter because individuals that exhibit normal sexual development and function can possess the sex chromosomes of the opposite sex: XY and YY females and XX, WX, WY, and even WW males. Kallman showed that the interactions of the sex chromosomes with specific autosomal factors played important roles in such often highly predictable events. He also convincingly laid to rest the phenomenon of sex reversal in swordtails from functional female to functional male.

In 1973, Kallman, Martin P. Schreibman, and Valerie Borkoski announced the discovery of a sex-linked gene in *Xiphophorus maculatus,* the alleles of which determined when the pituitary gonadotrops were activated and, thus, the onset of sexual maturation of males and females (Kallman et al., 1973). Inasmuch as the release of androgens terminates growth, early-maturing males were significantly smaller than late-maturing ones. So far, 9 different alleles have been identified in this species (Kallman, 1989). The polymorphism of this gene differed in each of the 10 species of *Xiphophorus* that Kallman studied. Moreover, it was associated with such phenomena as sexually active dwarf males or giant ones that never matured. Some species had 2 genotypes of differently sized males, which exhibited very different mating behavior patterns. Kallman's discovery of this sex-linked gene added a new dimension to our understanding of fish growth.

The color patterns of the common platyfish have been studied intensively by fish culturists, geneticists, evolutionists, pigment-cell biologists, and cancer researchers. Undoubtedly, Kallman's contributions to our understanding of the inheritance of coloration and pigmentary neoplasia in *Xiphophorus* provided basic data on which many of these

studies rest (Kallman, 1975; Vielkind et al., 1989). In making these discoveries, he stood idyllically on the shoulders of his mentor, Myron Gordon. Furthermore, on a practical level, many of us are indebted to him for generously supplying us with his fishes for our studies.

Kallman's interest in the platyfishes and swordtails has shifted to their biogeography. During 56 trips to Mexico and its neighboring countries, he has collected and observed more of these fishes in their natural habitats than anyone else. In particular, he critically studied their distribution in relation to the history of the fresh waters they now inhabit and did in the past. He described at least five new species and witnessed the natural extinction of at least one (Rosen and Kallman, 1969; Rauchenberger et al., 1990). To hear him expound on the subject, with map in hand or vista in view or in mind, is a rare treat. Kallman has traveled with and continues to assist dozens of researchers on collecting trips. Undoubtedly, every one of these individuals can attest to his extreme determination, planning, incredible perseverance, and physical stamina. On numerous occasions, he has outperformed hikers 30 years his junior on treacherous slopes within cloud and rain forests, in deep valleys and deserts. Although Kallman now is Professor Emeritus, he continues to work with *Xiphophorus* and is preparing several manuscripts that will become prominent contributions to the scientific body of knowledge.

Kallman always has maintained that to perform well professionally, one must think of his or her occupation not simply as a job, but as an avocation. His avocation was, is, and always will be research with the *Xiphophorus* fishes.

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