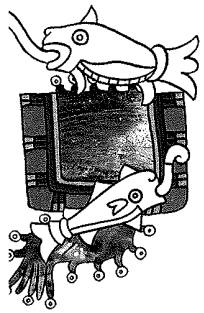
In recognition of Klaus Kallman for his outstanding contributions on the genetics of viviparous fish



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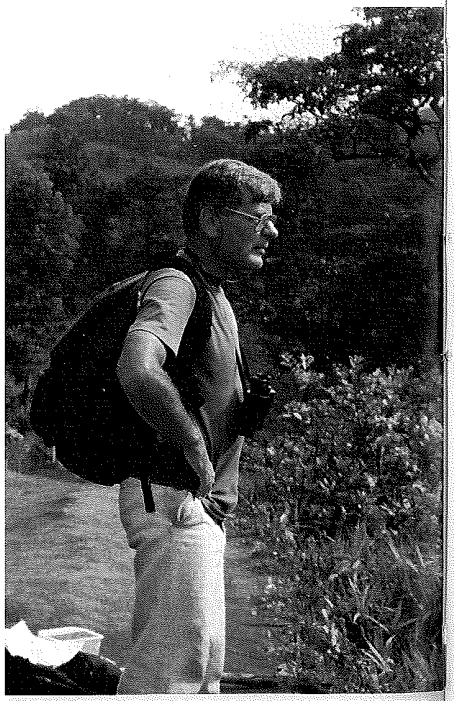
In a keynote address given at the 1st Aquatic Models of Human Disease Conference (San Marcos, TX) held in 2000, Klaus Kallman detailed the trials and tribulations of his mentor, Myron Gordon as he began his many ventures into Mexico in the 1930's in search of *Xiphophorus* fishes. Those fortunate enough to have been in attendance were entertained by factual stories of frontier crossings in Model T Fords, forging rivers and boulder strewn roads, countless disappointments, and ultimately the joy of lifting a seine out of a remote Mexican stream and seeing shimmering jewels of *Xiphophorus* fish reflected in the sunlight. Although Kallman was speaking of Gordon's exploits he did so with intimate familiarity. For it was Kallman, who over a 40 year career, ventured deep into the drainages of Mexico and through his genetic studies in both the laboratory and the field defined the biogeography of this group of poeciliids.

As a doctoral student at Cornell, Myron Gordon started the *Xiphophorus* Genetic Stock Center (*X*GSC; see Kallman, 2001) and later solidified the center upon moving to the Battery in Castle Clinton, Manhattan Island, New York, in 1938. In 1953, as a new graduate student at New York University, Klaus discovered the fish laboratory and convinced Gordon to sponsor his doctoral studies. At the time of Myron Gordon's death in 1959, Klaus and two other students sponsored by Gordon where within weeks of finishing their New York University doctoral studies; Donn E. Rosen, James W. Atz, and Klaus D. Kallman. All three went on to become internationally recognized fish geneticists (see Atz and Kazianis, 2001; Kallman, 2001). However, it was Kallman who had learned the details of the many intricate fish crosses that were always taking place in the *X*GSC and because of this knowledge he stepped up and became director of the *Xiphophorus* laboratory. For the ensuing 35 years Klaus supervised, enlarged, and enhanced the *X*GSC collection. During this time, he personally advanced and professionally promoted an extraordinary expansion in our understanding of *Xiphophorus* fish. In these years, Klaus would see the number of known *Xiphophorus* species climb from 6 to 22 and the known range traversed from Mexico across the isthmus into Central America. Many of the new species would be discovered and described by Klaus as a result of his relentless trips (over 55 trips) into the coastal drainages and rain forests of Mexico and Central America.



Born in Germany in 1928, Klaus Kallman achieved his Biology degree from Queens College, New York, in 1952. His doctoral work in Myron Gordon's laboratory led to a Master's Degree in 1955 and Ph. D. in 1959, working out details on immune systems in fish. Klaus had use of inbred *Xiphophorus* strains to test his ability to transplant fins (and other organs) from one fish to another as a method to study fish immune systems. In his first set of seminal studies, he showed that fin transplant rejection could be used to assess the genetics of histocompatibility in fishes (Kallman and Gordon, 1957, 1958). He was able to demonstrate that the "genetic laws of tissue transplantation" are operative in fishes and document that accelerated allograft rejection occurs upon secondary transplantation (Kallman, 1960; Kallman, 1970a) he also used tissue graft experiments to document self-fertilization in several fishes (*Rivulus, Poecilia, Gambusia,* and others; Kallman and Harrington, 1964; Kallman, 1962, 1963). These studies although interesting on their own merits, become impacting due to Kallman's thoughtful discussions of how such histocompatibility factors relate to population structure in the wild (Kallman, 1964, 1966, 1970a).

Although Klaus Kallman's publications comprise a rich set of literature dealing with an extensive variety of subjects, there are still two interwoven lines of investigation that hallmark Klaus' research impact on fish genetics. The first may be broadly categorized as sexual determination mechanisms and the second are his novel studies into the complex inheritance of sexual maturation and adult size. Both of these subjects most certainly spring from oversight of the *X*GSC and his many trips to Mexico observing natural *Xiphophorus* populations. The study of sex determining mechanisms in *Xiphophorus* turned out to be quite unique and interesting. Klaus has taught us that there exist many different modes of sex determination that are utilized among this species-rich group. If one begins making interspecies hybrids, these different mechanisms become readily apparent in highly skewed sex ratios that beg for explanation. Among various *Xiphophorus* species Klaus has documented XX/XY (Kallman, 1970b, 1989), WY/YY (Kallman, 1975), multiple sex chromosome mechanisms (i.e., WY, WX, or XX and XY or YY; Kallman, 1984), and in others, the existence of autosomal sex overriding mechanisms (Kazianis *et al.*, 2005). These studies, as all those published by Klaus, were undertaken with extreme care and precision. They reflect Klaus's unyielding scientific capability, and it is unfortunate that elegant genetic studies such as these will very likely never be duplicated in the current "rush to publish" scientific culture.

Perhaps, the most interesting and most impacting body of Kallmans' scientific works involved his detailed determination of the genetic control of *Xiphophorus* body size and time to sexual maturation. These works ushered in a new way of thinking about multigenetic or life history traits and truly showed one of many unique attributes of *Xiphophorus* fishes that make them an excellent experimental model.

As explained by Klaus (Kallman, 2005), "The fact that all individuals of a population mature at roughly similar ages and sizes, even when raised under different conditions, suggests that a complex genotype underlies sexual maturation. It is the result of long evolutionary history, and the phenotype *initiation of maturation* is integrated into the life history of the species."

Klaus' careful observation and extreme familiarity with the very large variety of *Xiphophorus* fishes allowed him to notice discrete differences in male adult body sizes. His genetics training drove Klaus to initiate crosses to try and determine the genetic basis for each size morphology. Working with several species (*X. maculatus*, *X. montezumae*, *X. multilineatus*, *X. nigrensis*, and *X. pygmaeus*), he was able to show inheritance of a Y linked series of alleles, termed P alleles (for pituitary gene), governed the age at maturation and thus adult body size (Kallman *et al.*, 1973; Kallman and Schreibman, 1973; Kallman and Borkoski, 1978, Kallman, 1989, 2005). The data presented in these studies, when placed in the context of mammalian literature, are quite staggering. For instance, in his investigation of nine different sex linked P alleles of *X. maculatus,* he identified genotypes that resulted in males becoming fully mature anywhere from 9.1 +/– 0.2 weeks with a resulting body size of 22.6 +/– 0.3 mm (i.e., Dr,Ir) to 29.3 +/– 1.8 (i.e., N^{1},Br) weeks with a body size of 39.3 +/– 0.7 mm (Kallman and Borkoski, 1978). Where these genotypes applied to average American males that reach a normal maturation (stage 5) at roughly 15 years of age and close to 1.8 m (5'9") we should see alternate genotypes walking around that do not mature until they are nearly 50 years old and attain a height of about 10 ft (3.1 m)!

In addition, should ultimate life span indeed be related to the length of time between birth and maturity the findings detailed in Kallman's studies may give us new avenues to explore the genetics of aging. At the very least his pioneering studies clearly show extreme alternative life styles and sexual behaviors may be exhibited among vertebrates that all share extensive genetic similarity. These classic and well-performed studies continue to stimulate students to ask approachable scientific questions about how biology adapts to environmental pressures.

Thus, looking back at the history of *Xiphophorus* research it seems quite clear that shipment of small fish from streams and arroyos in Mexico and Central America back to the New York Aquarium was only ripple effect of intellectual drive and the robustness of scientific spirit within two giants of fish genetics: Myron Gordon and Klaus Kallman. Over the 35 plus years Kallman ran the *X*GSC, he personally forwarded *Xiphophorus* as a model experimental system around which a vibrant and growing knowledge base would continue to build. So, it was indeed fortunate that Klaus Kallman found himself as "exactly the right person at the right place and time" (Atz and Kazianis, 2001), to assume oversight of the *Xiphophorus* system. But what circumstance led Klaus to this providence?

At the conclusion of his 2000 keynote presentations, Klaus was asked what brought him to *Xiphophorus* and drove him to become a premier fish geneticist of our time. His answer, "When I met Myron Gordon around 1953 or 1954, I knew nothing of tropical fishes; the only fish I had ever seen were on a dinner plate. But, I was already interested in genetics, even as a high school student and I always liked pretty things. This may be strange to say for a scientist, but flies turned me off and mice and rats turned me off too! But then, I met Myron Gordon, and I thought the fish looked beautiful. One did not have just a mouse in a cage but instead one could relate the fish to their natural habitat. This is what I liked to do, so it was ready made for me. I enjoyed every minute, and I am still enjoying it."

In speaking for so many who have worked with Klaus, have been inspired by him, and have been privileged to witness his excitement of investigation of these beautiful fishes, we have also enjoyed every minute of it! We are all better for it.

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