

Genetics of Japan, Past and Present

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In a review of the history of genetics in Japan, the name of Chiyomatsu Ishikawa comes first. Ishikawa was one of the few oldest graduates of the University of Tokyo who majored in zoology. He went to Germany as a postgraduate student, took his degree at the University of Freiburg, and served for some years as an assistant to Weismann. He later became professor of zoology in the College of Agriculture at the University of Tokyo and was a devoted disciple of Weismann and Weismannism until his death. The joint papers that Weismann and Ishikawa published in 1887, 1888 and 1889 (1) were concerned with the maturation and fertilization of the egg of the water flea. These papers dealt with cytological and genetical problems that might interest even some present-day investigators.

Among his pupils and associates in the College of Agriculture, Ishikawa had Toyama, who became an assistant professor under Ishikawa and taught sericultural science. Ishikawa apparently suggested that Toyama investigate the spermatogenesis and embryonic development of the silkworm. When the rediscovery of Mendelism was announced, both Ishikawa and Toyama took great interest in this new biological principle, and the latter immediately focused his studies on the heredity of various characters of the silkworm. Undoubtedly, the silkworm was one of the few animals suited for the study of Mendelism, for a number of varieties with respect to egg color, larval markings, and cocoon char-

acters had been isolated by the older breeders. Moreover, such a study promised to contribute something to practical sericulture.

Silkworm

Toyama's first paper on silkworm genetics was published in 1906 (2). This was one of the earliest papers on Mendelism in animals, including Bateson and Punnett's on poultry, Cuénot's on mice, and Lang's on *Cepaea*, the land snail.

One of Toyama's early works was concerned with the inheritance of cocoon color. He crossed a race that produced a white cocoon with a race that produced a yellow cocoon and found that the colors segregated in the progeny in typical Mendelian fashion. Toyama also worked on the inheritance of larval markings, egg colors and shapes, and some physiological characters. The most important and best known of Toyama's discoveries was the maternal inheritance, which he confirmed in the inheritance of certain egg-color types in 1913 (3).

Toyama also discovered the superiority in vigor and productivity of the F_1 hybrid between certain unrelated races. He had conducted for several years a large-scale experiment on this problem under the auspices of the Governmental Sericulture Experiment Station. The results were published in 1917, and confirmed the superiority of the F_1 hybrid in respect to growth rate, vigor, and quantity of cocoon fiber. He thus recommended the breeding of such hybrids to the breeders of the whole country. This was certainly a great discovery, some-

thing like that of hybrid corn from the practical viewpoint. Recently, I was informed of a hybrid strain of silkworm called J 122 established by one Nobu Nakazato. This strain is now recognized for various reasons as one of the best (or perhaps the very best) strains, and is being reared extensively in Japan. The value of the annual increase of yield due to the use of this strain is estimated at 3000 million yen, which is equivalent to \$8.3 million.

Toyama's untimely death took place in 1918 in the midst of an active life. His investigation of silkworm genetics was handed down to several younger workers. Tanaka took the leadership of this group. He is a graduate of Sapporo University. He became assistant professor of sericultural science in the same university. He later moved to Kyushu University and taught sericulture and genetics. He has devoted himself to the study of silkworm genetics and has made important discoveries. Many men who are now engaged in the genetics and breeding of the silkworm in various parts of Japan are Tanaka's former pupils.

The silkworm culture is an age-old, great industry of Japan; raw silk and silk fabrics had been the country's most important export goods for many years. Naturally, great effort was made to promote scientific studies of the improvement of sericulture and filature. A state institute on a fairly large scale devoted entirely to this purpose was established in 1911 and is still in existence. Several prefectures run local sericulture experiment stations. Three schools of college grade trained many young men for the practice or teaching of sericulture. These colleges now form parts of local universities. Really, no other insect among the many hundred thousands of species has been studied so intensively, and no other country has ever spent so much money for such a study. It is only natural that Japan is unrivaled in this particular field of study, and this is particularly true of the genetics of this insect. The bibliography of the comprehensive *Genetics of the Silkworm* (4) edited by Tanaka refers to nearly 1000 papers, of which at least 80 percent were written by Japanese investigators; and the majority are papers on genetics. Another book on the genetics of the silkworm, entitled *The Recent Advances in Gene Analysis of the Silkworm*

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(5) and written by five leading contemporary silkworm geneticists, enumerates 210 different genes that are distributed in 15 linkage groups. Thus the genetic studies of the silkworm form an important part of the contributions of Japanese investigators to the advancement of genetics in general.

If I mention the outstanding contributions made by our silkworm geneticists to genetical science in general, apart from Toyama's works that I have already mentioned, first comes Tanaka's discovery of the absence of recombination in the female, which is the heterogametic sex in moths. This phenomenon stands in contrast to the similar phenomenon known in *Drosophila*, in which recombination does not occur in the male sex. This discovery of Tanaka's in 1913 came very shortly after the discovery of the analogous phenomenon in *Drosophila* (6).

Next I may mention the mode of sex determination which was worked out more recently primarily by Hashimoto and Tazima (7). Sex determination in the silkworm is very different from that in *Drosophila*. It is extremely simple and clear-cut. The W chromosome is entirely responsible for this mechanism. The presence of a single W chromosome is sufficient to produce the female sex, irrespective of the number of Z chromosomes and autosomes. Thus,

2A + ZZ	♂	2A + ZW	♀
2A + ZO	♂	3A + ZZW	♀
3A + ZZ	♂ (?)	3A + ZZZW	♀
3A + ZZZ	♂ (?)	4A + ZZZW	♀
		4A + ZZZW	♀

Even combinations such as 3A + ZZW, 3A + ZZZW, and 4A + ZZZW have been found to be female. Tazima has endeavored to determine the exact locus of the gene or gene complex for the female sex. He obtained deletions of various parts of the W chromosome by means of x-ray irradiation and has obtained evidence that the gene or gene complex that is responsible for the mechanism of sex determination is apparently localized in a part of this chromosome. No conclusive data for the presence of a gene or a gene complex that is responsible for the male sex have been found.

The mechanism of sex determination is going to have a practical significance very shortly. In the silkworm, the male is considered to be superior to the female from a practical viewpoint. This is because the male larvae grow faster than the female larvae, the proportion of the fiber layer in the male cocoon is significantly greater than that in the female cocoon, and the fiber of the male cocoon is more uniform in its fine texture. Thus, if the sex of a silkworm can be distinguished in an early larval or egg stage,

it would be very valuable from the practical viewpoint. Tazima has obtained a strain having a piece of the second chromosome translocated to the W chromosome (8). This second chromosome piece carries the dominant gene "Sable," which gives the larva a characteristic sooty color and the egg a dark color. This character serves as the marker for the female sex. The young larvae that exhibit this color in this particular strain are invariably females. Tazima has succeeded in making this translocated piece so short that it does not interfere with the vitality of the insect. He has also succeeded in rearing a new strain in which the sex can be distinguished in the egg stage, by combining the translocated strain with another strain that is characterized by a light egg color. In this new strain, all dark-colored eggs are female, while all light-colored eggs are male. These eggs are laid in a mixture by heterozygous mother moths. The eggs are detached from the pasteboard as grains, and separated into two groups by using a machine especially devised for this purpose and utilizing a photoelectric effect.

For a general survey of the contribution of silkworm genetics to the sericultural industry, I may quote a recent note by Yokoyama (9), who is at present director of the Government Sericulture Experiment Station. In this note Yokoyama compares the figure for 1911 with that for 1951 in respect to the total yield of raw silk, on the one hand, with the total amount of the eggs used for the culture and the total area of the mulberry plantations, on the other. The yield of raw silk happened to be nearly the same in these two years, while the amount of the eggs used in 1951 was only 19 percent of the amount used in 1911, and the land area of mulberry plantation in 1951 was only 40 percent of that in 1911. These facts plainly show the extent of the improvement that has been accomplished by our geneticists in the breeding of the silkworm.

Goldfish and *Oryzias*

Next to the silkworm, the animals that early Japanese geneticists used as materials for their studies were goldfish and another freshwater fish, *Oryzias* (*Aplocheilus*) *latipes*, which we call "Medaka." Toyama did some genetic work on the goldfish but did not get any striking results. His work was succeeded by that of Higurashi (10) and further by that of Matsui (11), both of whom worked in the Fisheries Institute of the Department of Agriculture.

Oryzias has an advantage over the goldfish in its smaller size, quicker de-

velopment, and in its hardiness. This fish is commonly found in rice paddies all over Japan. Its red and white varieties are often kept with goldfish in Japanese homes. Ishihara, who was a professor of human physiology in Kyushu University, did some work on the genetics of this fish, and published a paper in 1917 (12). More extensive breeding studies of this fish were conducted by Aida in Kyoto, and his paper appeared in the 1921 issue of *Genetics* (13). He disclosed in this paper the presence of a gene for red body color in the Y-chromosome and its transfer by crossing over to the X-chromosome. This discovery coincided with Winge's discovery that disclosed essentially the same fact in the tropical fish *Lebistes*. The paper of Aida interested all geneticists, for it clearly demonstrated the presence of a gene in the Y-chromosome and also crossing over in the heterogametic sex, neither of which had been demonstrated at that time.

Influence of R. B. Goldschmidt

An event that should not pass without mention in the history of Japanese genetics was R. B. Goldschmidt's sojourn in Tokyo. Goldschmidt visited Japan first in 1914 to collect materials for his work on *Lymantria*. He was an old friend of Ishikawa, whom I mentioned at the beginning of this article. After Ishikawa's retirement, Goldschmidt took his chair in the Agricultural College of the University of Tokyo and stayed there from 1924 through 1926. During this period, and after his return to Berlin, several young Japanese men studied genetics and cytology with Goldschmidt, and many of them completed their doctoral theses. Goldschmidt's relationship to genetics and geneticists in Japan is still intimate in various ways, and Japanese genetics has been indebted to Goldschmidt for guidance and encouragement for a number of years.

One of the outstanding works accomplished by Goldschmidt's students was Masui's discovery of a simple method of "sexing" young chickens. I have been informed that in the United States alone there are about 2000 men engaged in this work. How much labor and expense in poultry farms all over the world are saved by sexing young chickens by this method is difficult to estimate. However, it is certain that it is enormous.

Genetics of Other Animals and Man

Drosophila was brought first by myself in 1925 from Morgan's laboratory in Columbia University to the Zoological Institute of Kyoto University. Seven

or eight associates or students of mine worked on this material. Of these men, Kikkawa is probably best known, through his paper on the biochemical genetics of the eye colors of *Drosophila* and the eye and egg colors of the silkworm (14). He is at present in the chair of genetics of Osaka University, and he is now conducting interesting studies on the relationship of various metal elements to colors of animals and plants.

Besides these workers in the genetics of *Drosophila*, several other boys and girls in Kyoto University majored in genetics under me, studying materials as diverse as man, mouse, *Habrobracon*, *Trichogramma*, *Harmonia* (ladybeetle), *Colias*, *Ephestia*, *Aphiochaeta* (a dipteran), *Tigriopus* (a marine copepod), sea-urchins, and protozoa. It is a great pity that more than half of them died during or after the war. Japanese genetics has lost in them several promising young workers.

The study of *Drosophila* is also thriving under Moriwaki in the Metropolitan University in Tokyo. The genetic and cytological studies of Kawamura and his pupils in Hiroshima University with some lower vertebrate materials, such as frogs, salamanders, newts, and freshwater fishes, are also worth mentioning. They are investigating in these materials the problems of polyploidy and heteroploidy, as well as racial and sub-specific differentiation.

Animal cytology in Japan has had its center in Hokkaido University in Sapporo. Oguma started this center about 1920 and directed it for about 20 years. He was succeeded by Makino, who is now focusing his own and his pupils' studies on the cytological investigation of tumors.

In the field of human genetics, Furuhashi is one of the pioneers in the study of blood groups. He proposed in 1927, in regard to the inheritance of the ABO groups, a genetic theory (15) that is essentially the same as Bernstein's theory, but that was advanced independently of that author. Since then, Furuhashi and his associates have continued their studies on the blood types of man, as well as of animals, and have discovered several apparently new types in human blood. These discoveries were made independently of the studies of European and American investigators. The Japanese investigators are now endeavoring to check each type of their discoveries with some types recently reported by Western investigators.

I have collected pedigrees of hereditary diseases and abnormalities from the Japanese medical literature and compiled two monographic papers (16). As a result of this work, I have found that the Japanese people do not seem to dif-

fer much from Western people in the kind and in the mode of inheritance of such abnormalities, as well as in the incidence of the gene that controls each abnormality, but they often differ rather considerably in the incidence of genes that are responsible for normal (for example, blood types and eye colors) or subnormal (for example, dizygotic twinning, osmidrosis axillae) characters. This is only a very rough statement, but it seems to be applicable to genetic distinctions between human races in general.

Plant Cytology and Genetics

Among the pioneers of plant genetics in Japan was Ikeno, who was a professor in the College of Agriculture in Tokyo University. Ikeno is well known as the discoverer of the motile male cell (spermatozoon) of *Cycas* (17). The discovery of a similar spermatozoon in the *Ginkgo* by Hirase (18), which was made about the same time, was largely due to Ikeno's suggestion. Ikeno took an interest in Mendelism and conducted breeding experiments with *Capsicum* (red pepper), *Plantago*, and the rice plant (19). His book (20), written in Romanized Japanese and first published in 1913, contains a simple and clear presentation of Mendelism, something like Punnett's *Mendelism* that had been published 6 years previously. Also, Hoshino's studies on the genetics of the flowering time of peas and rice, published in 1915, is noteworthy, for it was one of the pioneer works in quantitative genetics (21).

Next I must mention the name of Fujii, plant geneticist and cytologist and a pupil of Strasburger. He took the first chair of genetics in Japan which was started in 1918 as one of the chairs in the Botanical Institute of Tokyo University. The majority of the present plant cytologists and geneticists we have are either Fujii's pupils or his pupils' pupils. Indeed, cytology is rather heavily represented in all branches of biology in Japan. The international organ of cytology, *Cytologia*, was started in 1929 under Fujii's editorship.

The contributions of Japanese cytologists, especially to the knowledge of polyploidy in various plant groups, are widely recognized. Kihara's pioneer work on genome analysis carried out with wheat varieties is highly important both from the theoretical and practical viewpoints (22). His synthesis of the cultivated breed from the cross of an emmer wheat with *Aegilops squarrosa* in 1944 (23) coincided with McFadden and Sears' essentially identical demonstration by a similar experiment. Kihara's ingenious breeding method for obtaining seedless watermelons is certainly a good

example of the direct application of genetic knowledge to practical plant breeding. I have been told that fairly large amounts of the "seeds of seedless watermelons" are exported from Japan to the United States every year.

The breeding of strains of rice resistant to low temperatures was accomplished by Terao and others and is an outstanding contribution of Japanese plant geneticists to agriculture, one comparable to the contribution of animal geneticists to sericulture. Imai's study on the genetics of the morning-glory (24) was among the best-known works of plant genetics that was published in the 1930's and 1940's.

I am afraid I shall be blamed for putting too much stress on animal genetics, especially silkworm genetics, and too little emphasis on plant genetics. This is because I am an animal and a human geneticist, and my knowledge of plant genetics is more limited than my knowledge of animal genetics, and also because very few of our silkworm geneticists have published their works in English or any other European language, whereas most of the plant geneticists and cytologists have written papers in English or German.

Evolution

Let me add a few words about the history of the permeation of the concept of evolution among the Japanese. This concept was first introduced to us by E. S. Morse, who was a pupil of Louis Agassiz but a devoted disciple of Darwin. Morse came to Japan in 1881 and became the first professor of zoology in Tokyo University. He gave popular lectures on Darwinism on many occasions and was heard with great interest. His work of propagating the evolutionary concept was taken up by Japanese biologists, notably by Ishikawa and by Oka. Because of the absence of religious prejudice in Japan, this concept found no obstacle in diffusing among the Japanese people.

Genetics Society of Japan

The Genetics Society of Japan was started in 1915 under the name of the Japanese Society of Breeding. It was discontinued for a few years after the publication of two numbers of its organ and was reborn in 1920 under the name of the Genetics Society of Japan. It has at present more than 1000 members. These members belong to one of the 16 branches distributed in various districts of the country. The branches hold local meetings at regular or irregular intervals. The society also holds general meetings

annually at different cities where these branches are located.

Genetics Institutes

There are four chairs of genetics in Japanese state universities, one in the Faculty of Science of Tokyo University, which I have mentioned already, another in the Faculty of Agriculture in Kyoto University, still another in the Faculty of Medicine in Osaka University, and the fourth one in the Faculty of Science in Okayama University. However, genetics forms an important part of the courses of the biology departments in most of the universities in Japan. Some medical schools also have lectures on genetics, although the hours devoted to genetics are unreasonably few.

The establishment of the National Institute of Genetics in 1949, at Misima, was an important event in the history of genetics in Japan. The institute has six departments. About 30 research members studying materials ranging from man to virus are occupied in various fields of this science. Although they are working under the pressure of severe handicaps as a result of various difficulties of present-day life in Japan, they

will undoubtedly produce in their studies something that will contribute to the future advancement of genetics—at least we are hoping so.

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World Symposium on Applied Solar Energy

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With the purpose of fomenting and accelerating solar energy research and utilization, the Association for Applied Solar Energy, the University of Arizona, and Stanford Research Institute sponsored the first World Symposium on Applied Solar Energy and the associated Conference on Solar Energy in Tucson and Phoenix last November. More than 1000 scientists, industrialists, and interested laymen gathered to listen to 130 papers and addresses and to discuss ways to use the energy of the sun. The meetings were made particularly significant by the large attendance from abroad. From all over the world, nearly every laboratory or organization concerned

with solar energy research sent representatives to Phoenix. Thanks to the Ford and Rockefeller Foundations, UNESCO, the Office of Naval Research, the U.S. Air Force, the National Science Foundation, and the National Academy of Sciences, 130 foreign delegates from 31 different nations were able to join their American colleagues in the Valley of the Sun.

The participants were also able to observe nearly 100 working exhibits of practical developments at a special engineering exhibit located in the strong Phoenix sunshine. Exhibitors from this country and abroad participated in this special event.

The significance of these meetings will probably be felt as an upsurge of activity and research follows the discussions and evaluations that took place. There is little doubt that the papers discussed, and the close relationships that were established among scientists, engineers, economists, industrialists, and businessmen will advance the day when we may rely more directly on solar energy.

The papers delivered at the conference in Tucson were more technical in nature, while those presented in Phoenix were of more general interest and served as an introduction to solar energy research for the many nonspecialists who attended the meetings. The subjects of the papers at both meetings can be roughly divided into three categories: (i) solar energy measurements; (ii) increasing the world's supply of energy (mechanical, electric, and chemical); and (iii) increasing the world's supply of food (for both animal and human consumption).

Within these categories, some papers were devoted to basic research considerations, some to engineering problems related to the use of solar energy, and still others to the economic and industrial significance of the technical possibilities of solar energy.

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