I first met C. C. Tan (Tan Jiazhen) in 1946 at the University of Texas in Austin where I was visiting at the time. He was there to give a seminar on “mosaic dominance” in ladybird (aka ladybug) beetles. I was particularly interested because of the similarity to the pattern expression of scute alleles in Drosophila melanogaster and was eager to talk to him about this and about his D. pseudoobscura work with Dobzhansky and Sturtevant. So we arranged to have dinner together. We went by trolley to a Chinese restaurant, Sam Wah’s, which I believe was the only one in Austin. He suggested that he order the food, since by speaking in the native language he could get us more authentic Chinese dishes. Alas, the waiter did not speak Chinese; his ancestors had emigrated several generations earlier. He summoned the cook, who it turned out didn’t speak Chinese either, nor English for that matter. I ended up ordering the food. A little over half a century later, Tan and I met again, this time in China. Of course he recalled the incident, and we relived an amusing episode. A lot had happened in the meantime, especially to him.

The pigment pattern of the ladybird elytra (hard wing covers, singular elytron) is remarkably polymorphic; different geographical regions show characteristic pattern frequencies (Tan 1946a). More than 200 forms had been identified by 1946. The differences in various geographical regions are so striking that classical entomologists had often classified them as separate species, even separate genera. Tan found that the entire range of patterns could be explained by variation at a single autosomal locus with 12 alleles. Hoshino (1940) had studied three additional alleles not found in the regions Tan studied, which fit into the explanation, so there were 15 alleles altogether and undoubtedly more to be discovered.

One allele, s (for succinea), is recessive to the others. It produces a background orange-yellow color, which may or may not have a number of dark spots. The location of spots is very specific; they may occur at any of 10 sites. The penetrance of s is variable, as is the size of the spots if they do occur. The penetrance and size of spots are greater at lower developmental temperatures.

The other 11 alleles produce a much larger amount of black pigment, which may cover almost all the elytron, and the location of the black pigment is constant for a particular allele. Each of these alleles is dominant to s, and each acts independently of the others. Thus, heterozygotes for two different dominant alleles are black in all areas that would be black in either of the two constituent homozygotes. Tan (1946a) called this mosaic dominance. The yellow areas are conditioned by the s allele. They may or not show small spots, depending strongly on the developmental temperature.

When the beetle emerges from the pupa, the entire elytron is yellow. The black pigment then appears gradually, starting at the edges. The sharp delineation of the pigmented areas, the independence of the individual alleles, the timing of the developmental pattern, and the effect of temperature made this promising material for the study of developmental patterns, and the work attracted a great deal of attention at the time. One hypothesis, introduced by Dubinin and Serebrovsky (Dubinin 1933) to explain mosaic dominance of the scute and achaete alleles in Drosophila, was called “step allelomorphism.” The idea was that the bristle patterns reflected subdivisions of the gene. But the sub-gene hypothesis created more problems than it solved (Sturtevant and Schultz 1931), so most of the discussion at the time concerned developmental patterns rather than domains within genes.

C. C. Tan was born in Zhejiang Province in China in 1909 and did his undergraduate work at Soochow University. (Soochow was known as “the Chinese Venice.”) Tan then did graduate work at Yenching University in Peking where two of the faculty, Ju Chi Li and T. Y. Chen, had been students in T. H. Morgan’s laboratory at Columbia University. Li carried out several cytological and genetic studies while in the Morgan lab (e.g., Bridges et al. 1936). Also, he had played football at Purdue University. I visited him in his office in Beijing.
assigned the task of making a cytological map of the chromosomes of *D. pseudoobscura*. He quickly became an expert and soon found that races A and B, as they were then called, differed by a large number of easily recognized inversions. (A and B are now called *D. pseudoobscura* and *D. persimilis*.) The inversions were so characteristic that they could be used as identifying markers for the two species, which are almost indistinguishable by external morphology (Tan 1935). Tan’s work grabbed the enthusiastic attention of Sturtevant and Dobzhansky, and they began immediately to study the geographical distribution of the various inversion types. This marked the exciting beginning of the great Sturtevant–Dobzhansky collaboration, which continued until gradually the two had a falling out and Dobzhansky moved to Columbia University. (For speculation as to the causes of the rift, see Provine 1981.) One notable result of this work was the use of overlapping inversions to infer the phylogeny of the different chromosome types. Tan also pioneered in studying the genetic basis of sexual isolation (Dobzhansky and Tan 1936; Tan 1946b). This work, and much more, was summarized in Dobzhansky’s (1937) *Genetics and the Origin of Species*, which became an instant classic. I vividly recall my excitement as a graduate student on first reading this book in early 1938. I thought it was the greatest thing since Darwin.

Among the discoveries at the time was a new species, *Drosophila miranda* (Dobzhansky and Tan 1936). For one thing, this species had a number of chromosomal inversions, including those of a hypothetical form ancestral to or intermediate between a series of *pseudoobscura* and *persimilis* inversion classes. Tan estimated that at least 49 chromosome breaks were required to explain all the differences between *miranda* and the others. More interesting, as a result of a translocation, an autosomal arm split off and was inherited solely in males. Thus, it behaved like a Y chromosome. This neo-Y, because of the absence of recombination in Drosophila males, was expected to degenerate. There was much speculation at the time as to why and how rapidly such degeneration would occur, but the kind of detailed analysis that can provide answers has been possible only recently (e.g., Bachtrog and Charlesworth 2002).

Tan continued to collaborate on evolutionary studies with Sturtevant and Dobzhansky (Dobzhansky and Tan 1936; Sturtevant and Tan 1937) and on developmental subjects with others (Tan and Poulson 1937; Gottschewski and Tan 1938). He was highly productive during his time in the United States, and he continued this on his return to China. In 1937 he joined the faculty of Chekiang University, which, because of the Japanese incursions, had been moved to a southwestern locale in Kweichow. During that time, Tan had support from the Rockefeller Foundation. Although he continued some Drosophila studies, his main emphasis returned to ladybird beetles. In addition to his work on mosaic dominance, he and his students performed

Two views of C. C. Tan. The photographs were taken during a visit to the University of Wisconsin in 1986. Included in the photographs are Seymour Abrahamson and Rayla Greenberg Temin.
large-scale studies on the racial variation and population structure. This was an exciting period for Chinese genetics and for Tan, who by this time had a worldwide reputation. He also monitored a number of students. Among them was T. C. Hsu, later to become famous for his happy discovery that treatment with a hypotonic salt solution makes individual human chromosomes much more distinct. This finding was important in ushering in the renaissance of human cytology, which flourished in the late 1950s. The Rockefeller Foundation also supported Tan for a return to the United States to consolidate his studies and write them up for publication (TAN 1946a,b). It was during this period that I saw him in Texas.

Returning to China in 1946, he made another trip abroad, in 1948. He was a member of the standing council of the 8th International Congress of Genetics, which met that year in Sweden. Alas, the Lysenko debacle in the Soviet world was taking hold in China. For the next 3 decades, Tan’s life was one of political upheaval, intellectual uncertainty, and personal hardship, mixed with shorter periods in which things went somewhat better. At no time, however, was he able to pursue the research he was really interested in.

During this period in China, orthodox geneticists were forced to conform to Lysenko’s Lamarckian views or else switch to another field. Maize geneticists told me of being sent to grow maize in cold climates, where the short growing season was totally unsuited. Not only were these workers predictably unsuccessful, they endured various hardships including malnutrition. Tan stopped teaching genetics and concentrated on evolution. He escaped political difficulties by emphasizing paleontology and the evidence of evolution, rather than mechanisms. Of course, the ladybird and Drosophila population studies had to be dropped; they were not “practical” enough.

The popularity of Lysenkoism is not hard to understand. It promised quick results without the necessity of learning the complicated rules of statistics, Mendelism, meiosis, linkage, and cytogenetics. And sometimes it was successful, since selecting the best individuals to use as parents works for various systems of inheritance. But such techniques as inbreeding and hybridization for corn breeding did not fit the orthodoxy. I think Soviet and Chinese agriculture lost some momentum for another reason: since R. A. Fisher was discredited as a Mendelist, his efficient experimental designs for field crops were not followed. Many Chinese geneticists and breeders were trained in Russia. Followers of Mendel and Morgan had a bad time.

Among the Mendelists was the population geneticist, C. C. Li, who had a growing reputation as a teacher and textbook writer. Several Chinese geneticists, whom I saw years later, remembered him and extolled his great skill as a teacher. His widely influential book (Li 1948) was beginning to catch on, both inside and outside China. But life was not good, and he was under great social pressure to conform. His wife, who had lived in the United States, was particularly unhappy. The Li family eventually contrived, despite hardships, to get out of China through Hong Kong. [As a poignant aside, I note that Li’s book was dedicated “to Jeff.” I often wondered who Jeff was. Later I learned (Spier 1983): Jeffrey was an infant son who died during the hardships of the Li family’s last days in China.]

In the United States, largely through the influence of H. J. Muller, Li accepted a position at the University of Pittsburgh, where he has been ever since—a decision neither he nor Pittsburgh has reason to regret. His reputation as a teacher continued to grow throughout the world. His book quickly became popular in the United States and went through several editions. He is held in great admiration and affection, and recently celebrated his 90th birthday.

During the period from about 1958 to 1966, the Lysenkoist and Mendelian views of genetics were permitted to coexist. That must have been terribly confusing for students. “Practical” research was permitted, and Tan wrote several papers on the effects of high-energy radiation on the chromosomes of the rhesus monkey. Tan described an incident from that time, which is revealing and also wryly amusing. An experimenter had treated cotton with a vital dye and reported inherited effects of the treatment in the next generation. Tan was sent to investigate and later discovered that a paper reporting these results had been submitted with his name attached. He adroitly explained, however, that he had tried to learn the techniques but had been unsuccessful. Since he had not adequately mastered the techniques, he did not deserve to be an author. So his name was removed, and his reputation among Mendelian geneticists was thereby preserved.

Then another blow fell. The period 1966–1976 was the time of the Cultural Revolution, “ten long years.” Again, these were hard times, and Tan wrote books during that period. Furthermore, he lost almost all contact with his colleagues abroad. Finally, in 1978 he was able to leave China and attend the 50th anniversary of the founding of CalTech’s Biology Division in Pasadena.

At last, in 1979 at the age of 70 when most people are retired, he was able again to do genetic research. Once more, he took up his study of ladybird beetles, finding more alleles and obtaining more population data. But this was no longer center stage. The molecular revolution had occurred during the eclipse of Chinese genetics, and genetics was going in new directions. Characteristically, Tan immediately became the leader. He was active in the search for harmful environmental chemicals, advocating the Ames system for testing possible mutagens and carcinogens. He was alert to molecular techniques and wrote about RNA amplification in heterosis. He wrote a number of essays and review arti-
articles on various aspects of genetics and evolution and the changes brought about by technical advances. He was an early advocate of the construction of a human genome library. He directed various studies on rice. He used mitochondrial DNA to study human variability. And much more. In his 70 years of teaching and research, despite the long interruptions, he has published more than 100 scientific papers—original research, reviews, translations, and essays. His overview of Chinese genetics (Fu et al. 1995) is a concise summary of a long history.

As early as 1952, Tan had moved to Shanghai to become Professor and Chairman of the Biology Department at Fudan University. He has remained there since, holding various high administrative positions. Now retired, he is honorary director of the Genetics Institute at that university.

In the 1980s and 90s the world of genetics in China made up for its neglect of Tan. He was showered with richly deserved honors. These are too numerous to list, but I shall mention a few. He was president of the Genetics Society of China, the Environmental Mutagens Society of China, and the Biotechnology Society of China. He was an officer, usually vice president, of the International Genetics Congress in 1948, 1983, 1988, and 1993. Finally, he was the major proponent and then president of the 18th International Congress, held in Beijing in 1998. Among his foreign honors are a distinguished alumni award from the California Institute of Technology, foreign membership in the United States National Academy of Sciences, foreign membership in the Japanese and British Genetics Societies, and honorary life member of the New York Academy of Sciences. Finally, in 1999 he received a unique honor: a planet was named after him, Planet Number 3542, discovered at an observatory of the Chinese Academy of Sciences. What other geneticist can claim this?

Tan’s volume, The Selected Works of Tan Jaizhen (Tan 1992), is a trove of interesting items, especially for those who can read Chinese. But pictures are the same in any language, and the book has some 45 pages of them, mostly in color, showing the gregarious Tan at various times of his life, along with almost a Who’s Who of geneticists that he met during his travels. The pictures represent two periods, with large gaps caused by Lysenkoism and the Cultural Revolution. The book is composed of a summary and sometimes the entire text of some 80 papers. The majority of the articles are in Chinese, but enough are in English to satisfy the language challenge. Included is a heart-warming tribute to his mentor, Dobzhansky, whom Tan never saw after 1948. This book is a wonderful way to see the breadth of his interest. Now, well into his nineties, he can look back on a career that has had far higher peaks and deeper valleys than most geneticists can claim. Despite hardships and setbacks, he has had a rich life. He has lived by his intellect and personality, and by his wits, both scientifically and politically. The Selected Works of Tan Jaizhen shows the fruits.

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LITERATURE CITED


