THE LEGACY OF MOTOO KIMURA

Population Genetics, Molecular Evolution, and the Neutral Theory: Selected Papers. Motoo Kimura. Naoyuki Takahata, ed. University of Chicago Press, Chicago, IL, 1994. 686 pp., illus. $80.00 (ISBN 0-226-43562-8 cloth), $29.95 (ISBN 0-226-43563-6 paper).

More than most fields in biology, population genetics has been deeply divided into an empirical branch and a theoretical branch, not unlike modern physics. Population genetic theory was created largely through the work of J. B. S. Haldane, R. A. Fisher, and Sewall Wright in the first half of this century. Motoo Kimura (1924–1994) was arguably the single most influential theoretical population geneticist in the second half of the century. Published shortly before his death, this book brings together some of Kimura's most important papers. Although best known for his work on the neutral theory of molecular evolution, Kimura made fundamental contributions to many basic issues in population genetics.

The collection was edited by Naoyuki Takahata, a theoretical population geneticist who coauthored several papers with Kimura. Because of his own expertise and first-hand knowledge of Kimura's work, Takahata was in a unique position to edit this volume. James F. Crow has written a short foreword that provides biographical background on Kimura as well as the historical context for Kimura's contributions. Crow was Kimura's doctoral advisor at the University of Wisconsin at Madison, and they later collaborated on several important papers as well as a book.

The 57 papers in this collection are grouped into 18 sections based on subject. A list of these subjects shows the wide range of Kimura's studies in evolution: random drift; fluctuation of selection intensity; population structure; linkage and recombination; advantages of sexual reproduction; natural selection; meiotic drive; genetic load; inbreeding; evolution of quantitative characters; probability and time of fixation; age of alleles and reversibility; intergroup selection; infinite allele, infinite site, and ladder models; molecular evolution; nucleotide substitutions; the molecular clock; and the neutral theory.

To readers familiar with Kimura only through the neutral theory, this book offers a chance to admire the breadth of his work. In the foreword, Crow writes:

> Kimura's work falls into two categories. First is his research in theoretical population genetics. Second is his neutral, random drift theory of molecular evolution. To most biologists the neutral theory is his major contribution, and indeed it has revolutionized the way we think about molecular evolution. Certainly this is what Kimura is best known for. Yet population geneticists—the insiders, the pros—are, if anything, more impressed by the power, originality, and ingenuity of his theoretical work. (pp. xii–xiv)

Indeed, Kimura wrote in one of his later papers (p. 405), "...my life as a scientist has been devoted to the study of diffusion models in population genetics, as influenced by the great work of Sewall Wright."

Kimura applied the diffusion equations to many interesting problems in population genetics, greatly extending the work of Wright. Well before the development of the neutral theory, Kimura was interested in stochastic processes. In 1955 he wrote a famous paper in which he gave the complete description of drift using the diffusion approximation. The figures from this paper, which show changes in the probability distribution of gene frequencies due to drift, can be found in any standard population genetics textbook. In later papers he extended the approach to study the joint effects of drift, selection, and other evolutionary forces.

Many of Kimura's results are fascinating and often not intuitive. He showed, for example, that in a closed breeding system, the maximal avoidance of inbreeding is not the best way to preserve genetic variability in the long run. With Maruyama he demonstrated that the time to fixation is the same for a deleterious mutation as for an advantageous mutation with the same absolute fitness, although the probability of these two events is extremely different. Kimura is also responsible for a number of models that are now standard in population genetics: the stepping-stone model, the infinite sites model, the infinite alleles model, and the ladder model. Though he was exclusively a theoretician, Kimura's work derives from consideration of fundamental biological problems.

Kimura first published his formulation of the neutral theory in *Nature* in 1968. In this short paper he argued that the observed number of amino acid substitutions between species (approximately two per generation) was incompatible with Haldane's estimate that the cost of selection would only permit one substitution every 300 generations. From this discrepancy he reasoned that many genetic mutations must be neutral—that is, they must have no effect on the phenotype. This idea immediately ignited a controversy. Theodosius Dobzhansky, for example, called it rubbish (Calder 1985). It is testimony to the strength of Kimura's theory that 25 years after he first proposed it, discussions about the neutral theory are still very much alive. The discussion no longer centers on whether or not the neutral theory is correct, but rather on the proportion of the genome to which the neutral theory applies. Provine (1990) has written that the difficulty people had in accepting the neutral theory initially came from an unwillingness to accept that the laws governing molecular evolution can be substantially different from the laws governing phenotypic evolution. Today this is accepted as standard knowledge, and for many it may be Kimura's greatest legacy.

For this volume, Takahata has written brief essays introducing each of the 18 sections. He discusses not only the major results from each paper but also subsequent work (including many recent studies) by others on the same subject. These essays are well written and useful for appreciating the depth of Kimura's influence.

The grouping of the papers into 18 sections is necessarily somewhat arbitrary (as Takahata warns in the preface), because some papers deal with more than one subject. Moreover, the sections disrupt the chronological order of the book. Although inconvenient at times, the arrangement is ultimately helpful in putting the papers in a larger context. The sections can be read in any order. Takahata has also provided a list of Kimura's major publications (totaling 161) at the end of the book. The papers that Takahata chose to include in this collection represent a good selection of Kimura's most famous and most cited papers.

The casual reader should be forewarned: Kimura's papers are not easy reading. Most papers contain a substantial amount of math. A knowledge of elementary calculus is necessary but rarely sufficient for understanding some of the more complicated results. Fortunately, Kimura usually strove to make his main conclusions clear in words as well as equations. Readers may also be comforted by the knowledge that as a young student, Kimura had difficulty understanding mathematical population genetics (Kimura 1985).

This volume is likely to be a useful reference for both theoretical and empirical population geneticists, although the latter are certainly likely to find much of it challenging. As an empirical population geneticist, I would have preferred additional commentary, explanation, and background material relating to each section. I suspect that this sentiment may be shared even more by those whose primary work is outside of population genetics. However, at $29.95 the paperback is reasonably priced and serves a useful function for the specialist in bringing together the major papers of an extraordinary population geneticist.

MICHAEL W. NACHMAN
Section of Genetics and Development
Cornell University
Ithaca, NY 14853

References cited

Calder N. 1985. The lottery of life: changing views of evolution and human progress. Pages 443–454 in Ohta T, Aoki K, eds. Population genetics and molecular evolution. Berlin (Germany): Springer-Verlag.

Kimura M. 1968. Evolutionary rate at the molecular level. Nature 217: 624–626.

______. 1985. Genes, populations, and molecules: a memoir. Pages 459–481 in Ohta T, Aoki K, eds. Population genetics and molecular evolution. Berlin (Germany): Springer-Verlag.

Provine WB. 1990. The neutral theory of molecular evolution in historical perspective. Pages 17–31 in Takahata N, Crow JF, eds. Population biology of genes and molecules. Tokyo (Japan): Baifukan Co. Ltd.

THE FASCINATION OF FLOWERS

Diversity and Evolutionary Biology of Tropical Flowers. Peter K. Endress. Cambridge University Press, Cambridge, UK, 1994. 511 pp., illus. $84.95 (ISBN 0-521-42088-1 cloth).

Floral biology and pollination are among the most appealing areas of biology, touching the lives of nearly every human being. For some, perhaps most, individuals the fascination with flowers is casual—admiring a lovely bouquet of posies or receiving a childhood lecture on "the birds and the bees." Others may seek a more detailed understanding of flowers, making their own investigations by watching flower visitors in gardens or in nature or by watching a television program on natural history. Then there are those of us who make our livings studying, teaching, researching, and writing about flowers. Peter Endress's detailed and scholarly book is likely to be of interest primarily to the latter group. Nonetheless, the nonprofessional botanist and the casual browser are likely to appreciate the beautiful line drawings and the fine scanning electron micrographs.

Diversity and Evolutionary Biology of Tropical Flowers contains detailed descriptions of every sort of variation in every floral part, many of which may be new even to some botanists and ecologists (e.g., polysporangiate anthers). Endress uses examples from tropical families, including many genera unfamiliar to a primarily New World botanist—I came away with a much wider appreciation for tropical plant diversity than I had before reading this book. Endress also does an impressive job of bridging the German–English terminology barrier, orienting the reader on the concepts of *gestalt* versus *bauplan*. He clarifies the usefulness of the term *blossom* to describe a structure that functions as a flower but organizationally may really be an inflorescence (e.g., *Poinsettia cyathia*) or part of a flower (one-third of an *Iris* flower).

This work is an admirable combination of anatomy, morphology, taxonomy, and ecology; after reading it, specialists in each of these areas are likely to have a heightened awareness of the implications of aspects of various features in the other disciplines. Endress's book presents the anatomy relevant to pollination and fertilization in much greater detail than does A. J. Richard's *Plant Breeding Systems* (1986). The literature review is extensive, relevant, and remarkably complete; especially useful is the citation of many classic and current works in German and French. The current relevance of Endress's book is enhanced, as well, by reference to many up-to-date works in English and many personal communication citations in the text.

Endress leads the reader on a tour through the floral parts, from the outside in. He then examines the arrangement of the structural units, which leads to categorization of floral structures into different morphotypes (e.g., trap flowers and flag flowers). The discussion of pollination (from biotic to abiotic) follows naturally, offering interesting detail on each taxonomic group. This coverage of pollinators is useful because "bee pollination" encompasses many different groups of bees that visit flowers for different reasons, just as "beetle pollination" includes flowers with vastly different attractants and rewards for curculionid weevils and carrion beetles; flowers specialized for different groups of bees (or different kinds of beetles) have different morphologies and are not all described by simply designating them bee flowers (or beetle flowers). Lepidoptera pollination is adequately discussed, giving attention in turn to hawkmoths, settling moths, and butterflies. Thrips, birds, bats, and nonflying mammals are included as well, with recent refer-