DROSOPHILA ANANASSAE

DROSOPHILA ANANASSAE

Genetical and Biological Aspects

Edited by
Yoshiko I. Tobari
Department of Biology, Faculty of Science,
Tokyo Metropolitan University, Hachioji, Tokyo, Japan

JAPAN SCIENTIFIC SOCIETIES PRESS
Tokyo

KARGER
Basel • Freiburg • Paris • London • New York • New Delhi • Bangkok • Singapore
• Tokyo • Sydney

© Japan Scientific Societies Press, 1993

All rights reserved. No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system, without permission in writing from the publisher.

Supported in part by the Ministry of Education, Science and Culture under Grant-in-Aid for Publication of Scientific Research Result.

Published jointly by:
Japan Scientific Societies Press
2-10 Hongo, 6-chome, Bunkyo-ku, Tokyo 113, Japan
ISBN 4-7622-6726-0

and

S. Karger AG
P.O. Box, CH-4009 Basel, Switzerland
ISBN 3-8055-5774-4

Sole distribution rights outside Japan granted to S. KARGER AG, Basel.

Printed in Japan

Preface
During the 1930's two eminent Japanese geneticists, Kikkawa and Moriwaki, initiated genetic research on Drosophila ananassae. They discovered that this species exhibited two unusual features not discovered in D. melanogaster: crossing over in males and hypermutability. In the 1950's, after World War II, Moriwaki and his colleagues began to reconstruct the genetics of D. ananassae, and a decade later, Hinton turned his attention to this species. Moriwaki and his colleagues primarily documented genetic and cytogenetic findings of crossing over in males. Hinton encountered the morphogenetically hypermutability system due to a transposable element. Langley became involved in D. ananassae genetics through characterization of the transposable element at the molecular level. Later, Tanda, Gorces, Matsubayashi, and Hori and their colleagues began to characterize the mutants caused by the insertion of the transposable elements. Owing to the efforts of these researchers, the interesting problems that had not been possible to solve with D. melanogaster have been answered. There has long been a need for a monograph to bring together the scattered published and unpublished findings for the useful information of geneticists. This volume is not a comprehensive review of the genetics of D. ananassae but a brief introduction to its morphology, life cycle, chromosomes, reference photomaps, linkage data and reviews of several significant topics. I hope it will prove valuable for geneticists who have been or will be studying the unique features of this species, and that it leads them to novel discoveries which can even revise the contents in the near future. Various chapters of the manuscript were critically read by Drs. J.F. Crow, L. Pierce, H. Matsubayashi, Ms. C. Otsuka, Mr. K. Yoshida, and members of Dr. S. H. Hori's laboratory. For their valuable suggestions the authors and I wish to express appreciation. I am particularly grateful for assistance provided by Ms. H. Yamaguchi during the preparation of this volume, and am indebted to the Ministry of Education, Science and Culture of Japan for its financial support.

December 1992 Y.N. Tobari

Contents

Preface v
INTRODUCTION D. Moriwaki xi

1 Life Cycle Y.N. Tobari and D. Moriwaki 1
   1. Embryonic Life 2
   2. Pre-pupal Life 4
   3. Pre-adult Life 4
   4. Fecundity and Longevity of Females 5

2 Morphology D. Moriwaki and Y.N. Tobari 7
   1. External Structures 7
   2. Internal Structures 12
   3. Egg, Larva, and Puparium 16

3 Geographical Distribution Y.N. Tobari 19
   vii

viii

4 Chromosomes Y.N. Tobari, B. Goñi, Y Tomimura, and M. Matsuda 23
   1. Mitotic Chromosomes 23
   2. Meiotic Chromosomes in Males 25
   3. Polytene Chromosomes 29

5 Linkage Maps Y.N. Tobari 49

6 Crossing Over in Males M. Matsuda, H. Sato, and Y.N. Tobari 53
   1. Genetic Control of Crossing Over in Males 54
   2. Genetic Factors in Natural Populations 63
   3. Temperature Effects on Crossing Over 64
   4. Relation to Mutation Rate 69
   5. Conclusion 69

7 Mutator Systems M. Matsuda 73
   1. Autosomal Dominant Mutator in the bri Stock 75
   2. Extrachromosomal Clastogenic ca Mutator 78
   3. Autosomal Dominant pc Mutator with Extrachromosomally
      Inherited Suppressor 83
   4. Discussion 86

8 Optic Morphology (Om) Mutations 89
I. GENETIC STUDIES OF Om MUTATIONS AND THEIR MODIFIERS
   S. Tanda, L.A. Leshko, and V.G. Corces 89
1. The Genetic Nature of Om Mutability 90
2. Om Mutations 93
3. Second Site Modifiers of Om Mutants 96

II. THE tom RETROTRANSPOSON
S. Tanda, L.A. Leshko, and V.G. Corces 100
1. Molecular Characterization of the tom Element 100

III. MOLECULAR ANALYSIS OF Om MUTATIONS
S. Tanda, L.A. Leshko, and V.G. Corces 107
1. The Om(1D) Locus 109
2. The Om(2D) Locus 777

IV. HISTOLOGICAL ANALYSIS OF Om MUTATIONS S.H. Hori 120
1. External and Internal Phenotypes of Mutant Imaginal Eyes and Optic Lobes 727
2. Eye and Optic Lobe Anlagen in Mutant Larvae 125
3. Changes during Pupal Development 129
4. Discussion 131

CONTENTS ix

9 Population Genetics 139
I. POLYTENE CHROMOSOME VARIATIONS OF DROSOPHILA ANANASSAE AND ITS RELATIVES
Y. Tomimura, M. Matsuda, and Y.N. Tobari 139
1. Pericentric Inversions, Translocations, Deficiencies, and Extrabands 142
2. Distribution of Paracentric Inversions 145
3. Populations in Papua New Guinea 146
4. D. pallidosa 147
5. Taxon-K in Kota Kinabalu 148
6. Conclusion 148

II. HETEROSIS AND FREQUENCY DEPENDENT SELECTION
Y.N. Tobari 151
1. Heterosis 152
2. Two-chromosome Interaction 155
3. Conclusion 760

III. ISOZYME POLYMORPHISMS M.L. Cariou and J.L. Da Lage 160
1. Overall Genetic Differentiation 762
2. Amylase Geographic Polymorphism 163
3. Discussion 768

IV. ORGANIZATION AND STRUCTURE OF THE AMYLASE GENE FAMILY J.L. Da Lage and M.L. Cariou 171
1. Genetic Experiments 171
In 1925 T.H. Morgan, C.B. Bridges, and A.H. Sturtevant summarized the available data from the study of Drosophila in a volume entitled “The Genetics of Drosophila” (1925). In the chapter, ‘Other species of Drosophila’ they included the following reference to D. caribbea Sturtevant (1916): “Sturtevant (1921) recorded an autosomal recessive, curved wing. The character resembled the curved of melanogaster or of simulans.” Kikkawa (1935) was able to determine (using a wild strain sent by Sturtevant) that D. caribbea was identical to D. ananassae, which was initially described by Doleschall in 1858. In the decade leading up to World War II genetic and cytological studies
of D. ananassae were successfully pursued in Japan and the U.S.A. B.P. Kaufmann carried out a series of valuable cytological studies (1936a, b; 1937a, b) on a wild strain of ananassae collected in Alabama. Following the suggestion of Dr. Yoshitaka Imai* to study some representative species of Japanese Drosophila, I collected an unfamiliar Drosophila in a Tokyo fruit and vegetable market in July of 1931. Since the physiological requirements and rearing

* Yoshitaka Imai (1894-1949) was an eminent geneticist well known for his genetic research on the Japanese morning glory. In 1927-28, he studied Drosophila genetics in Prof. Morgan’s laboratory at Columbia University (later of CALTECH). Returning to Japan, he became Professor at Tokyo Metropolitan Higher School, the predecessor of the present Tokyo Metropolitan University, where he guided his colleague, Moriwaki, in Drosophila genetics.

conditions of the “new” species (later identified as D. ananassae) were similar to those of D. melanogaster, I immediately started culturing this species and collecting mutants.

At this point in time, Hideo Kikkawa, in Prof. Taku Komai’s laboratory in Kyoto University, also began studying a “new” species, a stock of which had been brought from Formosa by Komai. Kikkawa determined that both his “new” and Moriwaki’s unfamiliar species were D. ananassae. Then Kikkawa and I began corresponding, exchanging information and mutants continuously.

D. ananassae is most abundant in tropical areas, but is not native to Japan. The flies I caught by chance in Tokyo were undoubtedly transported on a fruit shipment from Formosa. By 1938 Kikkawa and I had discovered and characterized over 100 mutations. In that year Kikkawa changed the emphasis of his research to the genetics of silkworms. All his ananassae stocks were entrusted to me in Tokyo. Meanwhile we (Kikkawa 1937b and Moriwaki 1937a) had independently discovered spontaneous crossing over in males, a most remarkable phenomenon specific to this species. High mutability, and bobbed mutations associated with the Y and the fourth chromosomes were also established as specific features (Kikkawa 1938, Moriwaki 1937b).

With the coming of World War II, this research on ananassae became impossible. Concerned that the valuable mutant stocks might be lost, I prepared four replicate sets and deposited them at four institutions for safekeeping. After the war, however, I learned that all the dispersed replicates (in Kyoto University, Hokkaido University, Korea and my own laboratory) had been lost. The habitat of this species, the southern districts including Okinawa and Formosa, were beyond our reach. We were able to obtain wild strains of this
species from Texas and Louisiana from Drs. Th. Dobzhansky and J.T. Patterson in 1948. Four mutants newly obtained from these American strains were reported in 1949 (Drosophila Information Service, No. 23). With the fortunate establishment of Tokyo Metropolitan University (based mainly on the “Higher School”) in 1949, I again had an active laboratory, and the next year I had an opportunity to study abroad. I stayed three months in Prof. Dobzhansky’s laboratory at Columbia University. On my return trip (visiting Austin, Pasadena, and Berkeley) I was able to obtain several wild stocks. Using these wild strains I resumed my ananassae work, and later received additional wild strains from various geographical regions.

Since then, my colleagues, students and I have conducted various kinds of research (viz., Moriwaki and Tobari, 1975). First of all, the collection of mutants grew and the analyzed mutants were in turn reported in the Drosophila

INTRODUCTION xiii

Information Service (Moriwaki 1968, 1970, 1971, 1972, 1973). By the mid 1960s, S.F. Raychaudhuri and members of his laboratory in India had found a number of mutant genes (1959). Most of those were sent to Austin (University of Texas) to be included in the stocks there. On a course somewhat parallel to our laboratory C. W. Hinton, of Wooster College, U.S.A., was responsible for much of the post-WWII development of the genetics of D. ananassae, making use of his own mutant strains, those from Austin, and some strains sent from our laboratory. Correspondence and exchange of stocks between Hinton and ourselves began in 1966.

Extensive studies of inversion polymorphism in artificial populations were conducted by our laboratory in Tokyo. Moriwaki et al. (1952, 1953, 1954, 1955, 1956b) reported that a pair of 2L chromosome arrangements, standard (\(\text{In2LA}^*\)) and its inversion (\(\text{In2LB}^*\)), reached equilibrium frequencies ranging from 48 to 60 percent standard arrangement, depending upon the localities from which stocks were sampled and the initial frequencies. An analysis of the fitness components was carried out by Moriwaki et al. (1956a) and by Ebitani (1971). They demonstrated the superiority of heterozygotes. A maternal effect on the rate of development of heterozygotes was shown by Moriwaki and Tobari (1963). Still another balanced polymorphic system has been found involving inversions 3L (Tobari 1962) and 3R (Moriwaki and Ito, unpublished).

In the polymorphic populations, a joint effect of heterosis and frequency dependent selection has been reported (Tobari 1964; Tobari and Kojima 1967, 1968; Kojima and Tobari 1969). Some interaction between chromosomes 2 and 3 on fitness has been found by Tobari and Kojima (unpublished). Puffing patterns of the salivary gland chromosomes of this species, the map of which was reconstructed, have been investigated (Moriwaki
and Ito 1969). The appearance of puffs was found to be correlated with the rate of development of the three karyotypes, In2LA/In2LA, In2LA/In2LB and In2LB/In2LB.

In the meantime, male recombination was rediscovered by Moriwaki and Tobari (1967), which promoted further investigations on this interesting phenomenon, the study of which had been interrupted by WWII. As Grow (1989) pointed out, “Drosophila is exceptional though not unique, in having no crossing over in the heterogametic sex. D. ananassae is the exception to the exception. Male crossing over had never been entirely lost, or perhaps has been

* Currently we use the standard (+ or ST) and In(2L)A instead of In2LA and In2LB, following Hinton (1970, and unpublished) who used the symbol In(2L)A for the inverted sequence of the standard.

xiv

regained. This species may provide a clue to understanding male meiosis in other Drosophila species.” Hinton and Downs (1975) demonstrated that in six of the seven male D. ananassae genotypes, first division cysts were found more frequently than those in second division, indicating the duration of meiosis I to be greater than meiosis II. This contrasts with D. melanogaster in which the incidence of first division, with diakinesis as the earliest stage detected, was only about half that of second divisions. In the meiotic prophase of spermatocytes of ananassae, the arms of chromosomes 2 and 3 form pachytene diplotene bivalents held together by chiasmata in postdiplotene stages.

Another unusual feature attributed to D. ananassae is remarkably high levels of chromosomal polymorphisms in natural populations (Dobzhansky and Dreyfus 1943, Freire-Maia 1961, Futch 1966). Grow (1989) noted, “This is puzzling in view of the male recombination; there is a suggestion that some mechanism restricts exchange within heterozygous inversions during spermatogenesis.”

Hinton and Downs (1975) reported that, in male inversion heterozygotes having high levels of genetically monitored crossing over, no unequivocal evidence was found for formation of either pachytene inversion loops or anaphase bridges and fragments. In D. ananassae the meiotic origin of crossing over in males has been confirmed by genetic data, i.e., equality of complementary crossover classes and an absence of clusters of recombinants (Kale 1969, Moriwaki et al. 1970). On the other hand, Hinton (1969) and Hinton and Downs (1975) have reported chiasmata in the meiotic prophase of spermatocytes, although they failed to detect any correlation between meiotic chromosome behavior and specific genes regulating crossing over in males. Matsuda, Imai and Tobari (1980, 1983) demonstrated the presence of chiasmata in TNG F1 (TNG wild
males X marker females) males at a frequency capable of accounting for the observed high recombination values. They proposed that recombination in males of D. ananassae is meiotic in origin and that the iso-site aberrations, also observed in TNG F1 males, are related to chiasma formation. Focusing on this problem, Goñi and Tobari (1984) have shown a positive correlation \((r = 0.90)\) between male recombination and chiasma frequency.

D. ananassae from six geographical localities in Southeast Asia were examined for the recombination frequencies in males (Moriwaki and Tobari 1979), revealing that male crossing over may be very common. Tobari and Moriwaki (1983) demonstrated a positive correlation between the Minute mutation and male recombination, suggesting the possibility that a series of inducers and suppressors is responsible for both these traits. Hinton (1983) reported that a dominant crossover enhancer combined with a dominant

**INTRODUCTION xv**

...
third volume (1975) included a chapter, ‘Drosophila ananassae’ by Y.N. Tobari and myself. King suggested we write the draft on ananassae jointly with Hinton. However, Hinton persuaded us to write it independently, since he had already been preparing a manuscript, ‘The Cytogenetics of Drosophila ananassae for the volume edited by Ashburner and Novitski. Unfortunately, it happened that Hinton’s manuscript was cancelled because our description was to be published in the Handbook. Hinton generously allowed us to refer to his review as we needed. His generosity has continued to the present and will be frequently apparent in the pages of this book. A number of his mutant descriptions are originally presented throughout. They are referenced as Hinton (unpublished),’ which means ‘The Cytogenetics of Drosophila ananassae’ (Hinton unpublished results).


Here, we wish to express our respect for Dr. Hinton and to heartily thank him for his generosity. We also take this opportunity to thank Prof. J.F. Crow of the University of Wisconsin for his kind and insightful historical note on the genetics of D. ananassae, ‘Fortunes of War’ (1989) and his years of encouragement to those of us working on the “strange” Drosophila.

Lastly, we sincerely regret to inform the reader that Dr. Hideo Kikkawa passed away on October 3, 1990. He was a most distinguished scientist, and was also a pioneer in the genetics and cytology of D. ananassae. Many facts cited in this book are attributable to him. We pray for the repose of his soul and respectfully dedicate this book to his memory.