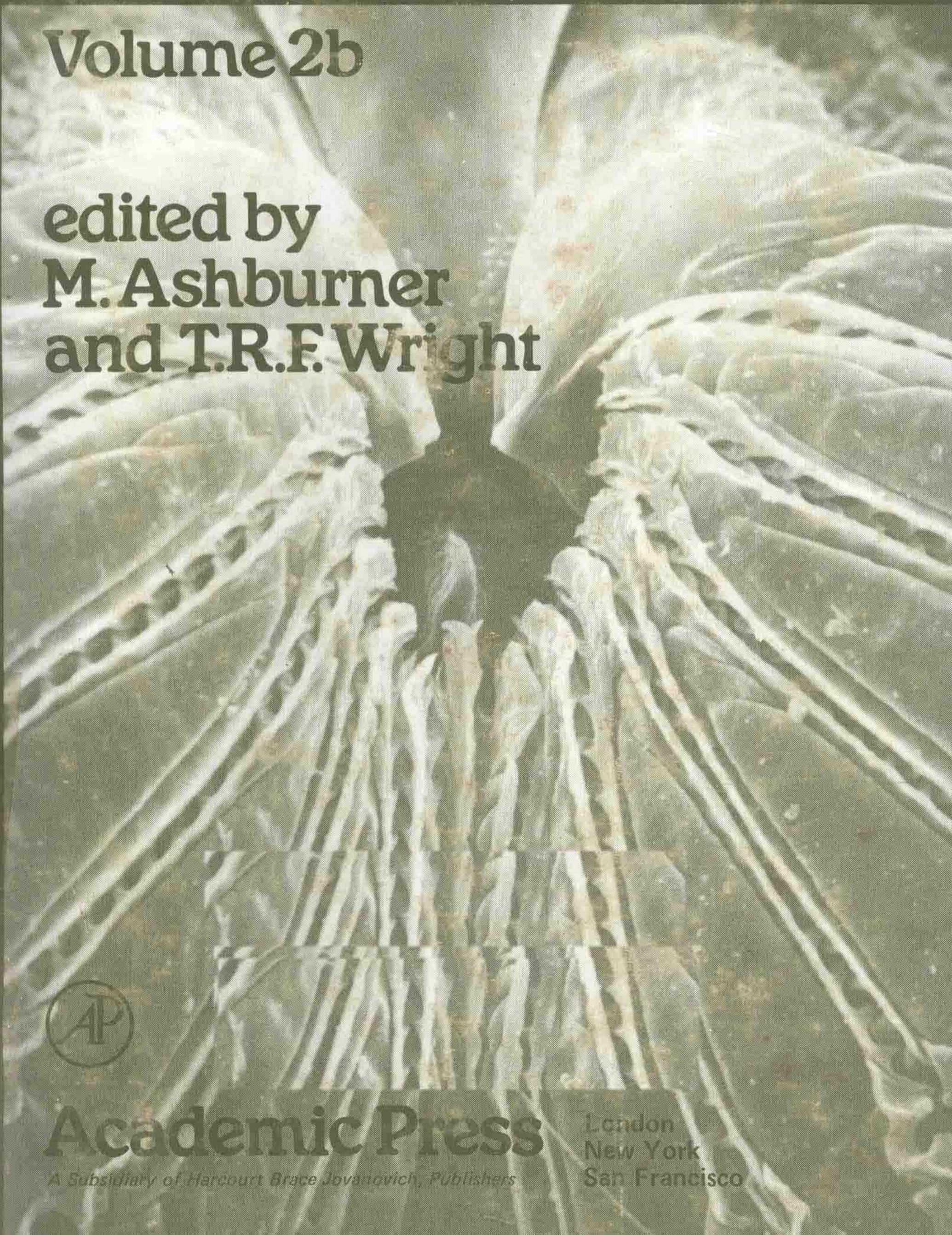
THE GENETICS AND BIOLOGY OF DROSOPHILA

Volume 2b

edited by
M. Ashburner
and T.R.F. Wright



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The Genetics and Biology of

DROSOPHILA

VOLUME 2b

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Preface

The importance of the fruit fly, *Drosophila*, for modern biological research cannot be overestimated. Research with *Drosophila melanogaster* is, of course, known best for its fundamental contribution to genetics. Indeed, it is perhaps no exaggeration to say that classical genetics is to a large part built on this foundation. It is a reasonable prognosis that *Drosophila* will also contribute significantly to our understanding of fundamental aspects of the molecular biology of eukaryotes. However, the significance of *Drosophila melanogaster* as an experimental organism extends to the farthest borders of biological inquiry. For example, biologists studying *Drosophila* are making major contributions to fields as different as neurobiology and evolutionary biology. The reasons for this include not only the vast storehouse of genetic information, but also the willingness of *Drosophila* biologists to share their knowledge and materials. In addition, many of the reasons for the success of *Drosophila* as an experimental organism will be seen from a perusal of the chapters of Volume 2 of this book. These include, for example, the ability to induce and select mutations which affect specific processes, the relative ease of creating mosaics by both genetic and surgical means, the hiatus between the determination and differentiation during the development of imaginal structures, and the usefulness of the giant polytene chromosomes for studies of the organization of the genome and gene activity. Last, but not least, *Drosophila* is easy and economical to culture, and it is now possible to obtain very large quantities of whole organisms of any developmental stage or their component cells and tissues, thus overcoming an objection hitherto made against *Drosophila* as an object for biochemical study.

This volume attempts to gather together as much information on the basic biology of *Drosophila* as possible excluding only its formal genetics found in Volume 1 and its population biology to be covered in Volume 3. The editors would like to emphasize that Volume 2 of *The Genetics and Biology of Drosophila* complements and does not replace the invaluable *Biology of Drosophila* edited by M. Demerec over 25 years ago.

Although the editors of Volume 2 originally intended that the chapters would appear in coherent groups and in a logical progression, the initial outline had to be abandoned to a certain extent in order to reduce, as much as possible, the lag time between writing and publishing by processing the chapters more or less in the order in which they were received. In spite of this and the fact that our coverage is not as comprehensive as we would have wished, we hope that these volumes will be of great value to *Drosophila* biologists and to others interested in the fundamental problems to which many of these chapters are addressed.

The editors were saddened by the deaths of three of our contributors, Ernst Hadorn, Hans Berendes, and Joan Whitten during the course of the preparation of this volume.

MICHAEL ASHBURNER
THEODORE R. F. WRIGHT

Cambridge, Mass.
August 1977

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The Editors would like to thank many of their friends and colleagues for their help in the planning and the execution of this venture. In particular we thank Peter Bryant, Sheila Counce, Antonio Garcia-Bellido, and Peter Lawrence for help with the organization of the several chapters. Invaluable help has also been given by many other colleagues in critically reviewing the chapters.

We would also like to thank Roger Farrand and Jenny Mugridge of Academic Press for their unfailing support.

Michael Ashburner in particular thanks Fotis Kafatos for providing him with congenial facilities at Harvard University which have not only made his task easier but also at times, pleasurable.

For their forbearance we thank our wives and families, and we promise them we will never do it again.

MICHAEL ASHBURNER
THEODORE R. F. WRIGHT

Cambridge, Mass.
August 1977

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10. Non-Sexual Behavior of *Drosophila*

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I. Introduction

A. Historical

The first publication to report use of *Drosophila* as an experimental organism dealt with the characterization of its behavioral responses (Carpenter, 1905). This is the first general survey of the non-sexual behavior of *Drosophila* since that time. For this reason, a number of older references have been included to indicate the antecedents of many current questions as well as to show the kinds of approaches that have been explored in the past. Additionally, these older reports do form the basis for much that is common knowledge in *Drosophila* laboratories. In the 70 years since Carpenter's work, the behavior of *Drosophila* has attracted the attention of workers in nearly every discipline of biology. The varied interests have incorporated a diversity of approaches and techniques including population sampling, the construction of ethograms and the development of instrumentation to record the electrical activity of single cells. The earliest work on non-sexual behaviour involved descriptions of reactions to a variety of stimuli. The effect of simultaneously presenting inputs of different sensory modalities was noted and found to be complex. Much of the work after that period used *Drosophila* as a test organism for analysing sensory input, especially visual input. The burgeoning of *Drosophila* genetics and systematics led to fragmentary reports, often incorporated in work of a different nature, concerning aspects of behavior. The past 20 years has witnessed use of *Drosophila* by workers interested in behavior *per se* and this period incorporated analysis of behavioral responses of a variety of activities. The relative ease with which various responses, such as phototaxis, can be quantified produced a literature on the measurement of the responses. More recent years have yielded analyses of the behavior of *Drosophila* species in the field and detailed analyses of sensory capabilities. Some of this latter work was a more sophisticated approach to responses used by earlier workers, but much of it represented a new approach based on the development of models to quantify input–output relationships of sensory mechanisms and motor activity. While mutants had been used over the years to explore aspects of behavior, or to quantify sensory input, the past few years have witnessed the use of mutations specifically induced in particular physiological systems subserving behavior. Underlying much of the work have been attempts to relate genetics and behavior, first at the level of how genetic lesions affect behavior and, more recently, the mode by which genes specify the neuronal interconnections responsible for motor output. Some studies have been couched in behavioral terms, others have not. The problems posed by earlier workers with respect to synergistic effects and heteromodal summation of stimuli are now receiving new attention, with the use of behavioral mutants and more sophisticated modes of analysis.

B. Behavioral Analysis

A "simple" condition of behavioral analysis, the identification and quantification of the requisite stimuli and their processing to produce a motor response, has not been met for many aspects of *Drosophila* behavior. Analysis of visual input has used an experimental system wherein the turning tendency or torque produced by a tethered fly can be related to the width and number of alternate light and dark stripes, their movement across the visual field and the light intensity of the stripes. In this case the carefully defined visual input can be related to motor output to predict how the fly will move in a particular environment. Other behavioral measurements have not incorporated detailed stimulus specifications. Yet for many behaviors information is available on the limiting factors or boundary conditions for the expression of particular stimulus–response relations. The level of behavioral analysis varies from noting that particular wavelengths of light are not perceived, and consequently play no role in behavioral responses, to characterization of increased sensitivity to particular wavelengths as a result of central nervous system processing. The general problem of integrative mechanisms involves a range of phenomena which have not been quantified. How does the CNS process information concerning a partially full crop, high light intensity and the smell of food into movement of legs and wings? Are all factors equally weighted or is there a subtle nonlinear algebra which produces locomotion. At a simpler level, how does a foot dipped in sugar cause proboscis extension. At yet a simpler level, how did the tarsus know it was sugar?

Many terms have been used in the literature to characterize particular modes of response. Various kineses, or increases in activity, have been described, with orthokinesis referring to a general increase in activity with increasing stimulation and klinokinesis indicating an increased rate of random turning (which may have the effect of decreasing stimulation). The taxes, or directed reactions, include klinotaxis and tropotaxis referring to, respectively, comparison of stimuli on two sides successively or simultaneous comparison of stimuli by symmetrically placed receptors. Teletaxis implies fixation and orientation towards one source of stimulation while photo- and geotaxis imply orientation with respect to the appropriate source of stimulation. Menotaxis implies the maintenance of a constant visual input by appropriate orientation. The prefixes hygro- and chemo- have been used to denote random or directed movement with respect to water or chemicals and thigmotaxis has been used to refer to the effect of contact with an object *per se*. These terms are used here to a limited extent since their use does permit quick reference to a more or less defined component. These terms, however, do not suggest a mechanism or an approach to analysis of a mechanism.

Analysis of some responses has involved use of appropriate instrumentation or modes of analysis which will be noted at the appropriate point. In spite of the range of analyses, there are aspects of *Drosophila* behaviour that are relatively untouched by physiological probing of the sensory basis of the behaviour or by a descriptive analysis of the response patterns.

C. Scope of Discussion

The literature survey is fairly inclusive and was completed in June, 1976. Many items that were of a preliminary nature and were subsequently presented in detail have not been noted. This is less true of some of the older literature. Where possible, the sensory input and central nervous system processing of information have been discussed together and in conjunction with available information on the genetic contribution to a particular facet of behavior. Where information on *Drosophila* is lacking for specific aspects of behavior, information gained from other higher Diptera has been used to assist in a more coherent presentation of non-sexual behavior. Unless otherwise stated all discussion pertains to *D. melanogaster*.

Data gained from one species has been used, in the literature, to interpret information derived from another species. There are many species of *Drosophila*. While species may share a physiological similarity, the expressed behavior in a particular environment may not be the same, even for closely related species An attempt has been made to indicate the species involved in any particular analysis. In some cases this has meant stipulating generic or subgeneric classifications. It is sufficient to note here that the genus *Drosophila* as well as several closely related genera each contains several subgenera.

Many aspects of non-sexual behavior are clearly related to sexual behavior, in terms of both sensory capabilities and integrative mechanisms. These have been discussed in the chapter on sexual behavior (see Chapter 11). An example is audition, which is more appropriately discussed under courtship behavior.

The link between physiological mechanisms and behavior is quite close and discussion of physiological analyses is included in the chapters dealing with *Drosophila* physiology. Included there are discussions of visual system mutations as well as the detailed presentation of electro-