

# THE GENETICS AND BIOLOGY OF DROSOPHILA

Volume 2c

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



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The Genetics and Biology of  
**DROSOPHILA**

VOLUME 2c

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The Genetics and Biology of  
**DROSOPHILA**

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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.

Cambridge, Mass.  
August 1977

MICHAEL ASHBURNER  
THEODORE R. F. WRIGHT

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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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## 19. Malpighian Tubules, Rectal Papillae and Excretion

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### I. The Malpighian Tubules

#### A. ANATOMY

*Drosophila melanogaster* possesses two pairs of Malpighian tubules, as do many Diptera. The right pair of tubules lies at the anterior end of the abdomen, and the left pair lies in the posterior (Fig. 1). Each tubule pair unites to form a common ureter, which enters the intestine between mid- and hindgut.

The anterior pair of larval tubules is divided into three different segments: a dilated initial segment, a short bent transitional segment, a long main segment and a short ureter (Fig. 2). A distinct transition between these segments does not exist, it is gradual. The shape and length of the tubules changes in the pupa: the tubules are shorter; the anterior segment becomes shorter and swells into a more or less globular expansion. This expansion



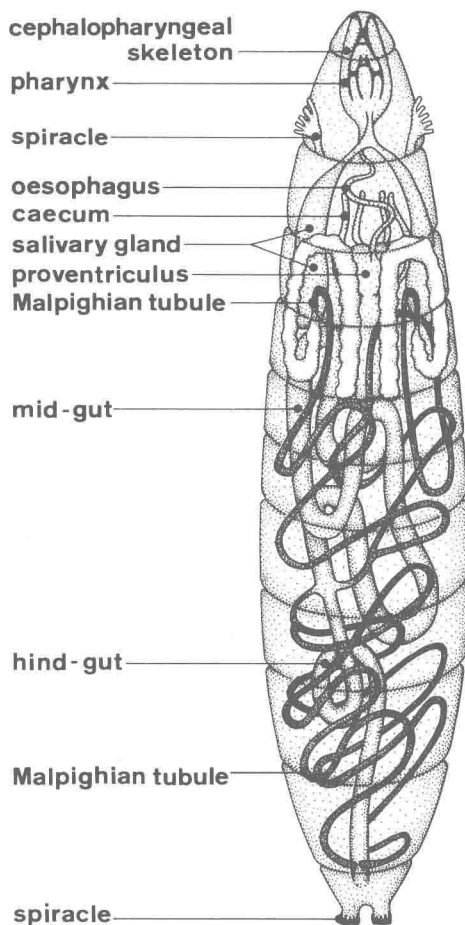


FIG. 1. Schematic presentation of the digestive tract and its accessory organs of the larva of *D. melanogaster*.

gradually disappears after the imago hatches. The Malpighian tubules of the imago do not show such a distinct segmentation (Fig. 3).

The ureter, like the gut, is surrounded by longitudinal and circular muscles. Besides secretion pressure, peristaltic contractions of these muscles drive the urine into the lumen of the gut. The posterior tubules of the larva and pupa lack segmentation; only a ureter can be distinguished. In the larva the tracheae seldom border on the tubules except on the ureter. On the other hand, tracheae are associated with the tubules more often in the adult.

The tubules lie unconfined in the body cavity, surrounded by the

