Atlas of Drosophila Morphology

Wild-type and Classical Mutants

Sylwester Chyb
Nicolas Gompel

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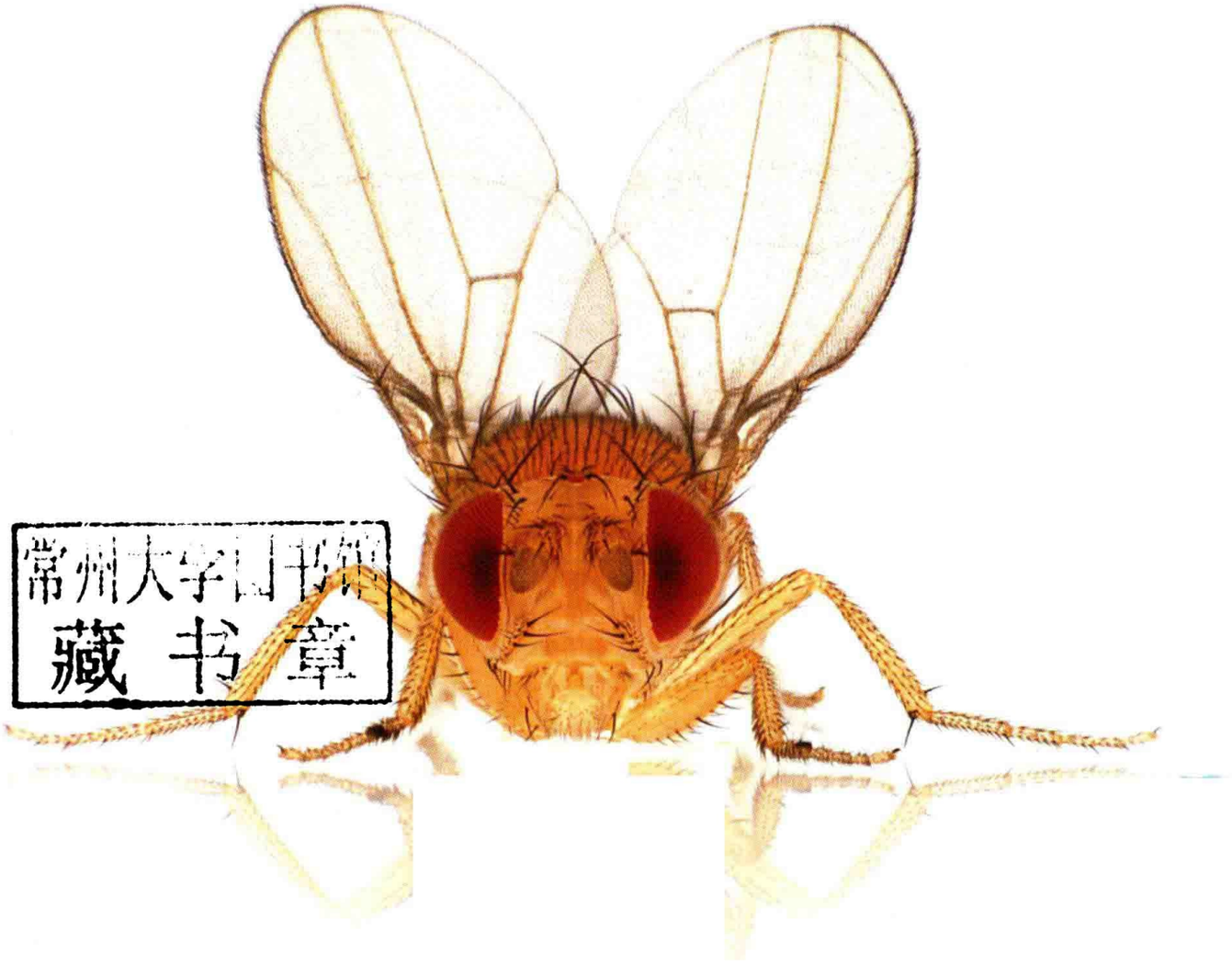

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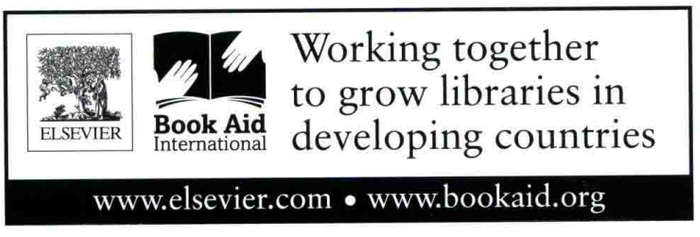

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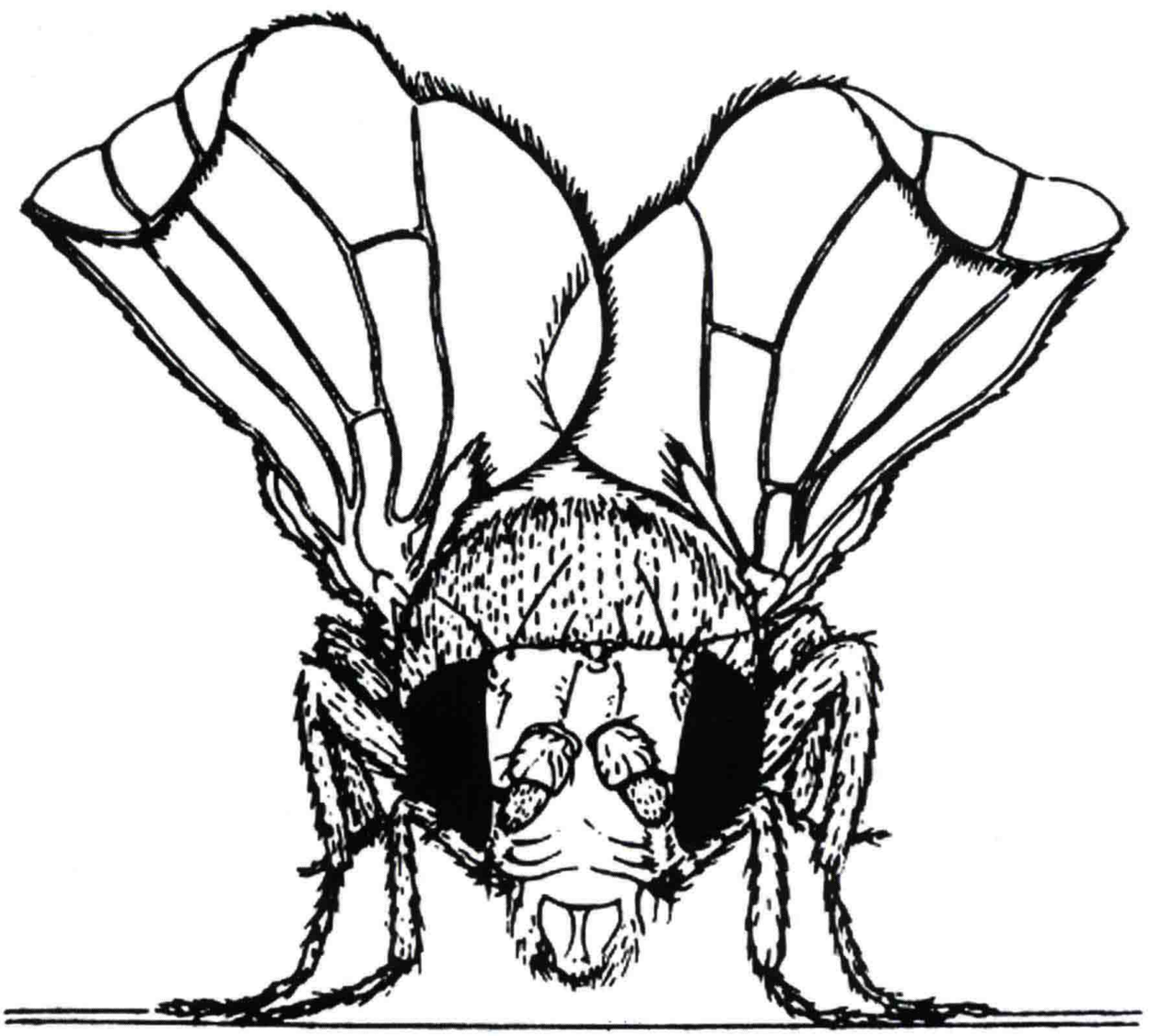


We dedicate this book to Marta (Sylwester),
and to Elora and Ingrid (Nicolas)

Foreword

Of course, there is hardly anything that has missed the digital revolution. FlyBase has come to dominate those of us who do fly genetics so much that it is hard to recall the old days. I first started thinking it was time to switch to *Drosophila* in about 1971 and I went to Madrid to be taught fly lore by Antonio Garcia Bellido and his students such as Ginés Morata and Pedro Ripoll. The "Red Book" by Lindsley and Grell (later Lindsley and Zimm) was our bible, copies were so much used that they fell apart after a year or so. The wonderful drawings of Edith M Wallace were an indispensable part of that book; for us they were essential to learn mutant genotypes and distinguish phenotypes. Then in the last two decades we have turned to our computers for genotypes, names, chromosomal locations, papers on particular genes, but for the mutant phenotypes, to first get to know them and to follow them through the generations, we still often rely on the tattered old Red Book and Wallace's drawings.

Up to now photographs of *Drosophila* have lacked impact and utility, mainly because of the limited resolution and depth of focus. For the photographer, *Drosophila* is the wrong size, too big for the compound microscope and too small for the macrolens. So in the past, drawings were better able to convey and emphasize points that helped recognition. But this new book has overcome these problems. The new methods of digitally accumulating focus planes combined with the skill of the authors have made the images staggeringly sharp and precise. Now you can explain to a new student how to see *Moiré*, an elusive but useful marker, perhaps even when you have not learnt to see it reliably yourself, or the slight difference between the karmoisin and the wild-type eye color. The staging of pupae is a particularly useful example of how words can fail and pictures succeed.

Even more important, the photographs convey the beauty that lies in the intricate detail of the fly and can help us remember why we are biologists. And also can help us explain to others how the fruit fly is so much more than it first seems to the naked eye. I know of no better way of illustrating this by quoting a great *Drosophila* geneticist, Curt Stern:

> *For more than 25 years I have looked at the little fly Drosophila and each time I am delighted anew. When I see it under moderate magnification of a binocular microscope I marvel at the clear-cut form of the head with giant red eyes, the antennae, the elaborate mouth parts; at the arch of the sturdy thorax bearing a pair of beautifully iridescent, transparent wings and three pairs of legs; at the design of the simple abdomen composed of ringlike segments. A shining waxed armor of chitin covers the whole body of the insect. In some regions this armor is bare; in other regions there arise short or long outgrowths, strong and wide at the base and gently tapering to a fine point. These are the bristles. Narrow grooves, as in fluted columns with a slightly baroque twist, extend along their lengths*
>
> **Two or Three Bristles, American Scientist, 42, 213–247, 1954**

You only need to glance at this lovely book to see what he meant.

Peter A. Lawrence
Cambridge, England

Introduction

When, in 1910, a white-eyed mutant of Drosophila ampelophila (as the species was then called) appeared, there was nothing known at the time to indicate that this species gives rise frequently to mutant types, since these had not been seen in the numerous experiments previously made.

T.H. Morgan, C.B. Bridges and A.H. Sturtevant,
The Genetics of Drosophila, 1925

Few could have predicted the career of a 3 mm long, tropical fly that was introduced into the United States by accident in the late nineteenth century and by the end of the following century had "invaded" biological laboratories worldwide. Even fewer would have envisaged the experimental power of this insect, and the universal knowledge it would bring to humanity. It has helped us understand heredity, genes, chromosomes, developmental patterns, immunity, physiological processes, population genetics, evolution, and has served as an experimental model to study human disease.

The quote above comes from one of the very first books on *Drosophila*, containing beautiful and precise pencil sketches by E.M. Wallace (like one reproduced here on the frontispiece). The Atlas you have in front of you takes advantage of the power of the digital photography available today. But the flies remain the same. In fact, many of the mutants illustrated in this Atlas were obtained within the first 5 years of work with *Drosophila* in the famous Fly Room (Sturtevant, 1965) at Columbia University, under the supervision of T.H. Morgan, and bred as stocks since. Numerous other mutants were induced following the discovery of the mutagenic effects of irradiation by H.J. Muller (Muller, 1930), another colorful member of the Morgan laboratory.

While the early publications on *Drosophila* are often accompanied by the illustration plates depicting the mutant phenotypes, this trend has progressively disappeared, and this information has become difficult to find as books went out of print. The rationale of this Atlas is to provide a modern version of this increasingly difficult to find information.

We hope this Atlas will become a useful resource in many genetics laboratories and help train students. If we managed to make entry into the *Drosophila* research even a bit easier then our goal has been achieved.

Sylwester Chyb and Nicolas Gompel
Cambridge, England
July 2012

How to use this book

Wild-type morphology

The external morphology of the wild-type flies is limited to the body parts affected by the mutant phenotypes. It also provides information on sexing flies and staging pupae. The information on anatomy is extracted, to a large extent from Demerec (1950) but we aimed to adhere to the current terminology by following the FlyBase guidelines.

Markers

The main part of the Atlas is devoted to about 70 mutants commonly used as markers. Their selection was based on our personal experiences, those of our colleagues who run stock collections as well as the availability of stocks expressing a single phenotype.

Markers are compiled into sections dealing with bristles, wings, appendages, eye shape, eye color, and body. Within each section, we introduce the markers in an alphabetical order based on the gene symbol. In a few instances, we have given preference to the traditional name of the mutant (e.g., *Hu*, *If*, *Sco*) rather than that of the gene, because of its more common use.

Below the marker name is the FlyBase gene or aberration number, together with available information on its location: chromosome (X, 2, 3 or 4), chromosome arm (L or R), cytological band, recombination map, and genomic coordinates (FB2012_04, released July 6, 2012).

A short description of the phenotype follows, highlighting the diagnostic morphological features of each mutant. Where abbreviations are used, these have already been explained in the wild-type morphology section.

The photograph plates face the text and illustrate phenotypes. Images were not intended to be exhaustive, as many markers are pleiotropic, but again sufficient in scope and details to show the key features of the phenotype(s). Most marker plates deal with a single allele, the most commonly used one if possible. On most plates we provide the images of the corresponding wild-type character (WT) serving as a reference.

We often show different magnifications and levels of details of the same character. The region shown at high resolution is boxed with a dashed line on the corresponding lower resolution image. We also highlight relevant details and morphological changes with arrowheads.

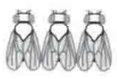
Many mutant phenotypes may be subject to modification with age, temperature, or genetic background and, accordingly, we attempted to illustrate the range of observable phenotypes. Phenotypes may also vary between individuals. These variations are described by the notions of *penetrance* and *variation in expressivity*.

Penetrance refers to the number of individuals of a given genotype that have the mutant phenotype. It can be complete (100% penetrance, i.e., expressed by all flies carrying the mutation) or incomplete (<100%). We have annotated the markers on an arbitrary scale of penetrance as full (100%), partial (<100%) and low (≪100%). This is only indicative and meant to prepare the users not to be surprised to find only a few flies of a given genotype displaying the expected phenotype.

Variation in expressivity refers to the extent to which the morphology is affected by a mutation. For instance, a mutation affecting wing size can result in no wing at all, a small wing, or a nearly normal wing, depending on genetic background and the rearing conditions. Here too, we ranked the markers on an arbitrary scale using a fly icon:

 All flies displaying the phenotype look alike

 The phenotype shows some variability, in a narrow range

 The phenotype is extremely variable

In the last entry for a marker we indicate whether it is easy to score (identify) or requires experience; we also comment on any overlap between the marker phenotype and that of the wild-type or any other mutants.

Summary plates

The marker section is followed by several summary plates where various mutants affecting the same body part are presented on one plate for easy comparison.

Balancer chromosomes

As markers are most often encountered via the use of balancer stocks, we included a section listing the most common balancers: their markers (dominant and recessive) as well as basic information on their structure (breakpoints and diagrams). We also illustrate a selection of double-balancer stocks most commonly ordered from the Bloomington Stock Center (K. Matthews, personal communication). For more information on the use of balancer chromosomes refer to Greenspan (2004). For general information on balancers and other rearrangements, see Lindsley and Zimm (1992) or flybase.org.

Drosophila melanogaster subgroup species

Finally, we illustrated the 9 species that together constitute the *Drosophila melanogaster* species subgroup. With the genomes of most of these species available, more and more researchers are starting to use other *Drosophila* species for their studies, which we felt warranted inclusion of a separate section.

Resources

Literature cited

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Greenspan, R. J. (2004) *Fly Pushing: The Theory and Practice of* Drosophila *Genetics*. 2nd edition. Cold Spring Harbor Laboratory Press.
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Morgan, T. H., Bridges, C. B. and Sturtevant, A. H. (1925) The Genetics of *Drosophila melanogaster*, *Bibliographia Genetica*2, 1–262.
Muller, H. J. (1930) Types of Visible Variations Induced by X-Rays in *Drosophila*, *Journal of Genetics* 22(3), 299–334.
Sturtevant, A. H. (1965) *A History of Genetics*. Cold Spring Harbor Laboratory Press.

Other printed resources:

Ashburner, M., Golic, K. and Hawley, S. (2005) *Drosophila*, A Laboratory Handbook. 2nd edition. *CSHL Press*.
Dahmann, C. (2008) *Drosophila*: Methods and Protocols (Methods in Molecular Biology). *Humana Press*.
Lawrence, P. A. (1992) The Making of a Fly: The Genetics of Animal Design. *Blackwell Press*.
Markow, T. and O'Grady, P. (2006) *Drosophila*: A Guide to Species Identification and Use. *Academic Press*.
Roberts, D. (1998) *Drosophila*. A Practical Approach. 2nd edition. *OUP*.
Sullivan, W., Ashburner, M. and Hawley, S. (2000) *Drosophila* Protocols. *CSHL Press*.

Online resources

www.flybase.org	Drosophila genes and genome
www.taxodros.uzh.ch	Drosophila systematics
www.flystocks.bio.indiana.edu/	Bloomington Stock Center
www.stockcenter.ucsd.edu	San Diego Drosophila Species Stock Center
www.dgrc.kit.ac.jp/en/	DGRC, Kyoto Stock Center
www.gen.cam.ac.uk/department/flylab/flyculture.html	Fly Culture

Technical notes

NOTES ON FLY STOCKS

Flies shown in this book were obtained from various sources: our personal collection, the Department of Genetics Fly Lab at Cambridge and the Bloomington Stock Center.

All flies were raised on cornmeal medium at 25°C, unless otherwise indicated. The staging was generally not taken into account, unless it was known to affect the phenotype, as for instance with eye color.

On several plates, the reader will notice variation in the color of the cuticle pigmentation, or the hue of the eye shade that is not highlighted in the text, or referred to as a particular phenotype. The origin of this variation is likely related to variation in the genetic background of the stocks.

NOTES ON PHOTOGRAPHY

Fly mounting

Adult flies and larvae were briefly anesthetized in vapors of ethyl acetate and mounted (glued) on a microscope slide. The appendages of adult flies were spread for esthetic needs, and the flies were further briefly anesthetized. The slide was placed on the microscope stage and the fly immediately imaged.

Lighting

To obtain an even, shadow-free illumination and maximize the contrast, a custom lighting system was made out of the conical shade of a desk lamp. The smaller top opening allowed the object to be seen from above. The inside of the cone was covered with strips of white light LEDs connected together, making a total of 96 uniformly distributed light points. The cone was placed above the object to be photographed, which was also surrounded by a small cylinder of tracing paper, to increase light homogeneity.

Imaging

The images in this Atlas were acquired with a ProgRes C5 camera mounted on a Leica M420 Macroscope. For each view, a stack of images of different focal plans was processed with the software Helicon Focus (HeliconSoft) to obtain an extended depth-of-field projection. The resulting projections were then enhanced using Adobe Photoshop.

Acknowledgments

The work in genetics has not been accomplished by any one individual or group of individuals, but has been worldwide and the outcome of many hands and minds.

T.H. Morgan, from his telegram read at the Nobel Banquet in Stockholm on December 10, 1933

There are numerous colleagues we would like to thank for their "hands and minds."

First and foremost, we wish to thank John Roote of Cambridge University, who put the two of us in contact in the first place, helped us shape this Atlas, and offered advice and unflagging support throughout. Alike, Kathy Matthews of the Bloomington Stock Center went out of her way in seeking for us these photogenic flies and providing advice and feedback at different stages in the development of this work.

We acknowledge the FlyBase team for organizing, curating, and maintaining a state-of-the-art database from which we have drawn extensively in the preparation of this Atlas.

Finally, we want to thank Peter Lawrence for agreeing to write an insightful foreword with the dual perspective of a fly geneticist and a photographer.

Each of us also wants to make personal acknowledgments.

Sylwek is grateful to Professor Roger C Hardie FRS who is solely responsible for converting him to fly-pushing, Professor James L Frazier whose sabbatical at Imperial College was the intellectual spark which led to this book, and Professor Stephen J Simpson FAA for enquiring about the book's progress in his unmistakably charming way. I also want to acknowledge my sons, Adam and Szczepan, for polishing my English. Very special thanks to Professor Roger Keynes as well as Fellows and Master of the Trinity College for extending to me the status of Visiting Scholar, and to Department of Genetics, University of Cambridge for granting access to the reserved collection of the *Drosophila* literature. And finally, many thanks to Kristi Gomez, Editor at Elsevier for whom nothing was a problem.

Nicolas is grateful to François Leulier, Benjamin Prud'homme, and Ilona Grunwald-Kadow for feedback, support and inspiration, to Claude Moretti for providing technical help with the imaging setup. Also to Igor Siwanowicz for great tips on image treatment, to Yann Moreaux for having been a wonderful coach in the use of Adobe imaging softwares, to Jessica Cande for kindly proofreading the manuscript, and to Karine Grimaldi for fruitful feedback and suggestions on the layout design.

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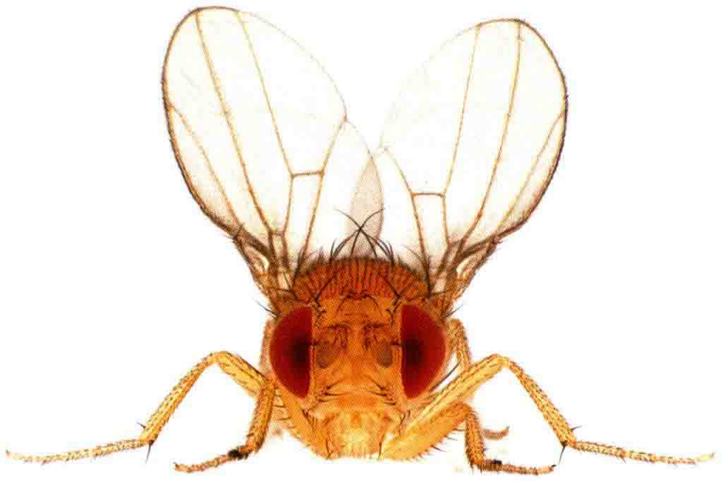

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