

of diapause; an unusually cool autumn may induce diapause sooner than would be expected based solely on photoperiod. The cue for diapause induction need not be received by the life stage that enters diapause. For example, in many species adults that experience short daylengths produce diapause eggs, while those exposed to longer photoperiods do not.

### See Also the Following Articles

Aestivation ■ Cold/Heat Protection ■ Diapause

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## Dragonfly

see *Odonata*

# Drosophila melanogaster

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When biologists refer to "*Drosophila*" they usually mean *D. melanogaster*. This small, inconspicuous species has become one of the premiere model systems in modern biology. Research on *D. melanogaster* over the past century has led to better understanding of virtually every discipline of biology, especially genetics, development, and evolution. This work has applications not merely to the biology of flies and other insects, but also into the causes of a variety of human diseases. The most powerful aspect of *Drosophila* as a model system is the ease with which its genome can be manipulated through a variety of genetic techniques, including germline transformation with transposons. The genomics revolution and the newly completed genomes of *Drosophila* species, including *D. melanogaster*, has made this genus a pivotal tool in understanding the evolution and working of the genome and an important model for bioinformatics and genome annotation. The next frontier in *Drosophila* research will be to link DNA and protein sequences with gene expression and function and these molecular genetic characters with ecological and evolutionary adaptations that drive species-level diversification in this group.

### HISTORY OF DROSOPHILA RESEARCH

*D. melanogaster* was first described by Meigen in 1830. Subsequent taxonomists described this species under 10 different names from 1830 to 1946. The profusion of names was likely due to the quick spread of this species throughout the world as a result of the fruit trade.

*Drosophila* research began in the early 1900s when a number of scientists, most notably T. H. Morgan, began to use *D. melanogaster* as a model organism for studies of genetics. W. E. Castle was the first to bring this species into the lab and develop many of the culture techniques still used today. It was Morgan's group at Columbia University, however, that fully took advantage of this species as a research model. Morgan, up to that time, had been experimenting with marine invertebrates in an effort to understand a number of developmental processes. He was looking for a small, rapidly developing species that produced large numbers of progeny and was both easy and inexpensive to maintain and manipulate in the laboratory. Early in these studies, it became clear that *D. melanogaster* was just such a model system. In 1912, Morgan's group had isolated roughly two dozen mutants. Morgan and his colleagues began to use these mutants to provide experimental evidence for the chromosome theory of inheritance, and they devised methods for gene mapping that are still used today.

*Drosophila* was an important model organism throughout the 20th century. Ed Lewis began working on homeotic mutants in the 1950s. His work focused on the bithorax gene complex. Most Diptera have only a single set of wings on the mesothoracic segment, but these mutant flies had two pairs of wings, one each on the meso- and metathoracic segments (Fig. 1). This set of genes has since proved to be the major control switch for body axis development and is conserved in many organisms, including humans. The Nüsslein-Volhard and Wieschaus screens of the early 1980s further advanced the use of *D. melanogaster* as a model system to study the development of more complex organisms. The future Nobel laureates elegantly showed the genetic control of development, mapping many of the genes involved in forming the major body axes in nearly all metazoans.

The genus *Drosophila*, and *D. melanogaster* in particular, continues to be an important model system in biological research. The *Drosophila* Genome Project completed the entire genome sequence of *Drosophila melanogaster* in 2000 and frequent updates and revisions of this genome have enhanced our understanding of heterochromatic regions, transposable elements, and gene expression. Recently, 11 other species of *Drosophila* have been sequenced (*Drosophila* 12 Genomes Sequencing Consortium, 2007). As of mid-2008, a reference search of the NCBI database (<http://www.ncbi.nlm.nih.gov/>) recovers



**FIGURE 1** The ultrabithorax mutant. [From Lawrence P. A. (1992). "The Making of a Fly: The Genetics of Animal Design." Blackwell Scientific Publications, Oxford, U.K., with permission of the publisher.]

over 30,000 papers with the query term “*Drosophila melanogaster*.” Furthermore there are over 850,000 nucleotide entries for this species. Several stock centers around the world are dedicated to maintaining live cultures of *D. melanogaster* and its relatives for research. For example, the Bloomington Stock Center (<http://flystocks.bio.indiana.edu/>) currently has about 20,000 different lines, mostly mutants of *D. melanogaster*, and the Species Stock Center (<http://stockcenter.ucsd.edu/info/welcome.php>) maintains about 2000 cultures from nearly 300 species in the family Drosophilidae.

## ECOLOGY AND LIFE CYCLE

*D. melanogaster* originated in tropical west Africa and has spread around the world, primarily through its commensal associations with humans. This species is a generalist and breeds in a variety of rotting fruits in its natural environment. It was first recorded on the east coast of North America in the 1870s following the end of the American Civil War and the expansion of the fruit trade.

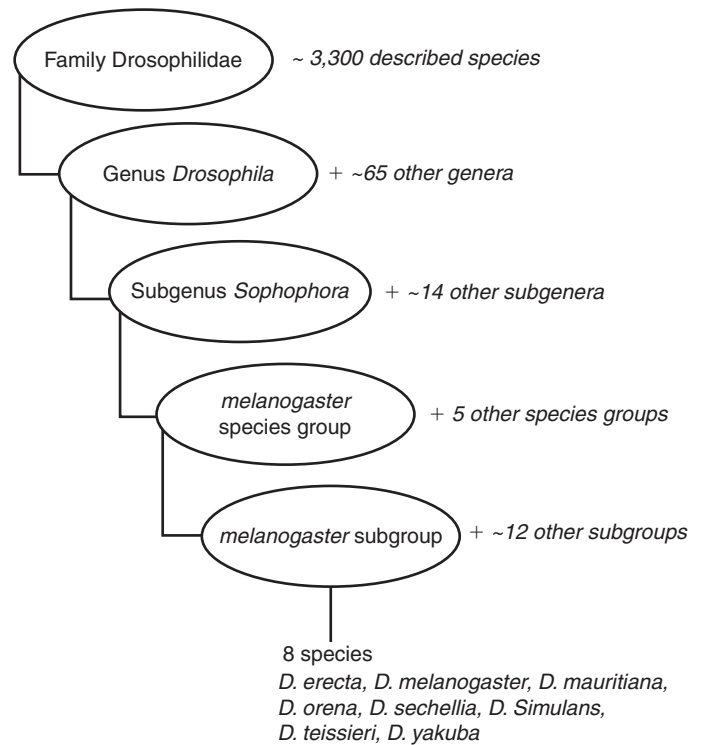
Like all other members of the family Drosophilidae, *D. melanogaster* is holometabolous and undergoes a complete metamorphosis. Development times vary, depending on temperature. Typical *Drosophila* laboratories maintain flies between 18 and 25°C. Stocks or infrequently used strains are usually kept at lower temperatures to slow development and reduce the amount of stock changing required. Complete development takes about 3 weeks at 18°C. At 25°C, embryonic development is completed roughly 1 day after the egg is laid. The fly then goes through three larval stages prior to pupation. Larvae are motile and work their way through the food media feeding on yeast and bacteria. After 4 days, the larvae enter a stationary pupal stage. Pupation takes approximately 4 days, after which time adults emerge from the pupal case. After they eclose, females require about 2–3 days to develop mature eggs. Therefore, at 25°C about 10 or 11 days is required to complete a cycle from egg to egg. At higher temperatures (29–30°C), pupal lethality and female sterility begin to have an effect on culture viability.

After the adult ecloses, it takes between 6 and 12 h for both males and females to begin mating. Genetic crosses require known paternity. Females are collected prior to reaching sexual maturity and isolated from males, so controlled crosses can be made. Mean adult life span is 40–50 days, although some individuals may live up to 80 days. A single female can lay as many as 75 eggs in a day, for a total of perhaps 500 eggs in a 10-day period.

## MORPHOLOGY AND PHYLOGENY

The family Drosophilidae is divided into a number of genera, subgenera, species groups, and species subgroups; this system gives each species a “taxonomic address” that loosely defines relationships within the family. For example, *D. melanogaster* is placed in the genus *Drosophila*, subgenus *Sophophora*, and *melanogaster* species group and subgroup (Fig. 2). *D. melanogaster* is a typical drosophilid and possesses a number of the characteristics, such as red eyes and plumose arista, that delineate this family. Along with the other taxa in the *melanogaster* and *obscura* species groups, *D. melanogaster* bears a single sex comb on its first tarsal segment. These are 7–12 thickened setae (hairs), which are closely set in a row, or comb. The number and position of the setae diagnose *D. melanogaster* from all but the most closely related species.

Within the Afrotropical *melanogaster* species subgroup, *D. melanogaster* is most closely related to the triad of species containing *D. simulans*, *D. sechellia*, and *D. mauritiana*, the common ancestor of which is thought to have diverged between 2 and 3 mya. *D. simulans*, a closely related species that is also cosmopolitan, can be differentiated



**FIGURE 2** Placement of *D. melanogaster* within the family Drosophilidae. [Modified after Powell, J. R. (1997). “Progress and Prospects in Evolutionary Biology. The *Drosophila* Model.” Oxford University Press, New York.]

only by examining the characters of the male genitalia, namely the number of prensisetae and the shape of the epandrial lobes.

## D. MELANOGASTER AS A GENETIC MODEL

Over the past 100 years, geneticists have built a large “toolbox” of specialized methods that allow them to manipulate the genome of *D. melanogaster* with more deftness than is possible with any other organism. These methods have largely taken advantage of some of *Drosophila*’s inherent characteristics, such as the lack of recombination in males. Some widely used techniques include polytene chromosome visualization and *in situ* hybridization, using balancers and other cytological aberrations for genetic crosses, and germline transformation using *P* elements and other transposons to examine gene expression and to tag genes for cloning.

The chromosomes found in the larval salivary glands are highly duplicated, allowing a characteristic banding pattern to be visualized with a compound light microscope (Fig. 3). Polytene chromosomes, which allow researchers to observe and study large-scale genetic rearrangements such as inversions, duplications, translocations, and deletions, have been used by geneticists to answer a variety of questions. Early work focused on understanding chromosome mechanics and using deletions to map the location of specific genes. Molecular geneticists have used the polytene chromosome in conjunction with *in situ* hybridization to more specifically localize the chromosomal site of specific cloned genes or gene fragments. For example, small fragments of DNA can be amplified by using the polymerase chain reaction (PCR), incorporating radioactive or bioluminescent probes



**FIGURE 3** Polytene chromosome of *D. melanogaster*: X, X chromosome; 2R, right arm of second chromosome; 2L, left arm of second chromosome; 3R, right arm of third chromosome; 3L, left arm of third chromosome; 4, fourth chromosome; CH, chromocenter. [From Krimbas C., and Powell, J. R. (eds.) (1992). “*Drosophila* Inversion Polymorphism,” Fig. 2B, p. 344. CRC Press, Boca Raton, FL, with permission.]

as labels and with hybridization to the polytene chromosomes. In addition, evolutionary and population geneticists have used inversion patterns to reconstruct the history of species and populations.

Balancers are multiply inverted chromosomes that repress recombination and are useful for making controlled genetic crosses as well as keeping homozygous lethal mutant genes in culture. In addition to being marked with a visible phenotype, such as curly wings, balancer chromosomes are often homozygous lethal, making crosses and the establishment of multiple mutant stocks much simpler.

Transposable elements (TEs) are native components of the genomes of nearly all organisms. TEs typically encode a protein, called transposase (some also move via a method that is mediated by reverse transcriptase), which can catalyze the movement of the element throughout the genome. Transposons have been used to mutagenize and clone genes, as well as to study spatial and temporal patterns of gene expression. The *P* TE was isolated after several researchers noticed an aberrant syndrome of hybrid sterility when certain geographic strains were crossed. This sterility was caused by the introduction of *P* elements into a genetic background lacking these transposons. This transposon has become the most versatile and widely used tool in modern *Drosophila* genetics.

Since their discovery, *P* elements have been heavily modified and are now used extensively to manipulate *Drosophila* germline DNA. The transposase coding regions have been removed and replaced with a wild-type marker gene, resulting in an inactive transposon with a dominant marker. It is possible to introduce such a *P* element into the germline of mutant embryos by injecting the embryos with cloned *P* element DNA and a buffer containing the active transposase. The offspring carrying the *P* element construct will have a

wild-type phenotype because the marker will rescue the mutant phenotype of the recipient strain. Such transformed lines can be used in mutagenesis screens by crossing the inactive *P* element construct line to a stock engineered to contain active transposase. Because *P* elements insert at random into the genome, they are very effective mutagenic agents and can insert into a gene, thereby disrupting its function. Once a phenotype has been observed, the transposase can be “crossed out,” leaving a stable *P* element insertion into a gene of interest. The mutagenized gene can be easily cloned by means of a variety of techniques (e.g., inverse PCR) because the sequence of the *P* element is known and a “transposon tag” is present in the gene of interest. Other powerful techniques that exploit transposons are enhancer trapping and the flipase recombination system.

### THE GENUS *DROSOPHILA* AS A MODEL SYSTEM

In addition to referring to the single species *D. melanogaster*, “*Drosophila*” can also refer to the entire genus *Drosophila*, a spectacular radiation of roughly 1500 described species. This genus can be found throughout the world in every conceivable habitat, from tropical rain forests to subarctic regions. Generally, these species are saprophytic, feeding and ovipositing in rotting plant and, sometimes, animal material. Members of this genus have been used as a model system for understanding evolutionary biology. A number of *Drosophila* groups, such as the *obscura*, *repleta*, and *virilis* species groups, have become prominent model systems in evolutionary biology. Such studies include chromosome and molecular evolution, the mechanisms of species formation, phylogeny, ecology, and behavior.

#### See Also the Following Articles

Chromosomes ■ Diptera ■ Genetic Engineering ■ Research Tools, Insects as

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