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# Introduction to *Drosophila*

Farzana Khan Perveen

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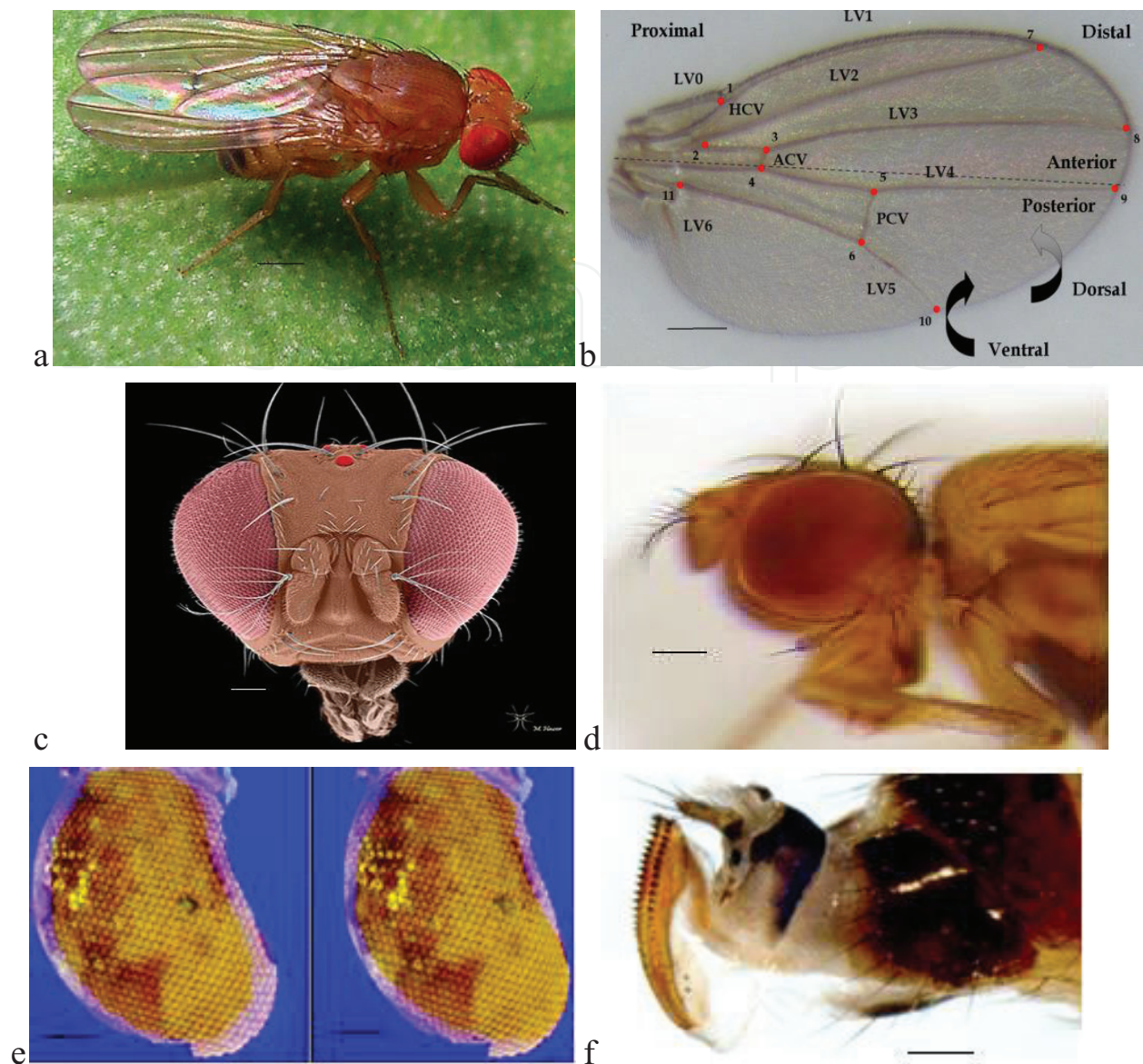
## 1. Introduction

*Drosophila* derived from the Greek word drósos means dew loving. They belong to the Drosophilidae family; and are most frequently known as fruit flies or often called vinegar, wine or pomace flies. Their main distinguishing character is to stay on fruits, which are ripped or rotten. There is another related family Tephritidae, their members are also called as true fruit flies or fruit flies. *Drosophilae* are different from them. They feed primarily on unripe or ripe fruits. Many species of *Drosophila* are agricultural pests, especially the Mediterranean fruit flies. They oviposit through ovipositor and capable of colonizing in live fruits that are still in the process of ripening, causing massive agricultural damage (**Table 1; Figure 1a and f**) [1, 2]. Currently, the genus *Drosophila* is considered as paraphyletic group. The entire genus, however, contains more than 1500 species [3], which are very diverse in their appearance, behavior, and breeding habitat [4]. However, many members of the family Drosophilidae are categorized into two subgenera, in which around 1100 species belong to *Drosophila* subgenera, moreover, about 330 species belong to *Sophophora* subgenera including *D. (S.) melanogaster*. Furthermore, another *Drosophila* species, i.e., Hawaiian spp. have more than 500 species in which only 380 species are described. Furthermore, they are occasionally documented as a separate subgenus or genus, i.e., *Idiomyia grimshawi* [5], but this is not widely accepted. About 250 species are part of the genus *Scaptomyza*, which arose from the Hawaiian *Drosophila* and later recolonized in continental areas [6]. However, *Drosophila* spp. are distributed all over the earth; moreover, many species are found in the tropical regions. Furthermore, the alpine zones, cities, deserts, swamps, and tropical rainforest also confine them. Furthermore, hibernation takes place in many northern species [7].

Their breeding takes place in numerous types of rotten vegetation and mycological materials, comprising barks, flowers, fruits, mushrooms, and slime fluxes. However, the maggots of *D. suzukii* act as the pest and feed on fresh fruits. Moreover, some species of *Drosophila* have achieved the status of parasites and predators. Furthermore, several species attract to lure of mushrooms and fermented bananas, but others deny attracting to every type of bait. Furthermore, females and males are assembled for mating on appropriate propagating

<b>Kingdom:</b> Animalia
<b>Subkingdom:</b> Invertebrata
<b>Division:</b> Eumetazoa
<b>Subdivision:</b> Ecdysozoa
<b>Superphylum:</b> Tactopoda
<b>Phylum:</b> Arthropoda
<b>Subphylum:</b> Atelocerata
<b>Superclass:</b> Hexapoda
<b>Class:</b> Insecta
<b>Infraclass:</b> Neoptera
<b>Subclass:</b> Pterygota
<b>Superorder:</b> Endopterygota
<b>Order:</b> Diptera
<b>Family:</b> Drosophilidae
<b>Subfamily:</b> Drosophilinae
<b>Tribe:</b> Drosophilini
<b>Genus:</b> <i>Drosophila</i> Fallén, 1823
<b>Type species:</b> <i>Musca funebris</i> Fabricius, 1787
<b>Synonyms:</b> <i>Oinopota</i> Kirby & Spence, 1815
<b>Subgenera:</b>
<ul style="list-style-type: none"><li>• <i>Drosophila</i></li><li>• <i>Sophophora</i></li><li>• <i>Chusqueophila</i></li><li>• <i>Dorsilopha</i></li><li>• <i>Dudaica</i></li><li>• <i>Phloridosa</i></li><li>• <i>Psilodorha</i></li><li>• <i>Siphlodora</i></li></ul>

**Table 1.** Taxonomic rank of the fruit fly, *Drosophila* spp. Fallén, 1823.



**Figure 1.** Adult of the fruit fly, *Drosophila* spp. Fallén, 1823 (Diptera: Drosophilidae) (a) [9]; wing morphology: ventral view of left wing and landmark positioning; LV: longitudinal vein; HCV: humeral cross-vein; ACV: anterior cross-vein; PCV: posterior cross-vein; the proximal, distal, anterior-posterior, and dorsal-ventral axes are shown (b) [10]; head, frontal view (c); lateral view of head shows characteristic bristles above the eye (d); stereo images of *Drosophila* (e); ovipositor of an adult female spotted wing drosophila, *Drosophila suzukii* (Matsumura), lateral view (f); photographs (c)–(f) by courtesy of Martin Hauser, Department of Food and Agriculture, California, USA; bar on photograph: 25 cm.

materials separate from breeding sites to form leeks. Also, many *Drosophila* spp., comprising *D. immigrans*, *D. melanogaster*, and *D. simulans*, are found neighboring and accompanying with humans and are called domestic species. Also, human activities, such as transporting of fruits and other fresh food items, are responsible for introducing many species throughout the world, including *D. immigrans*, *D. melanogaster*, *D. simulans*, *D. subobscura*, and *Zaprionus indianus* [8].

### 1.1. Morphology

Most *Drosophila* spp. are small, about 2–4 mm long, but some are larger than a house fly. They are typically pale yellow to reddish brown or black and transverse black rings across the abdomen with brick red eyes. Many species have distinct black patterns on the wings (**Figure 1b**) with plumose (feathery) and arista antennae, bristling on the head and thorax (**Figure 1c** and **d**) [11]. The characteristics of wing venations are used to diagnose the family. *Drosophila* flight path of straight sequencing with rapid and jerky turns of the wings with intersperse between positions of rest is known as saccades movement. However, when it turns in saccades movement, it can be revolved at the angle of 90° in about 50 milliseconds. Moreover, *Drosophila*'s wings can beat 220 times per second [12].

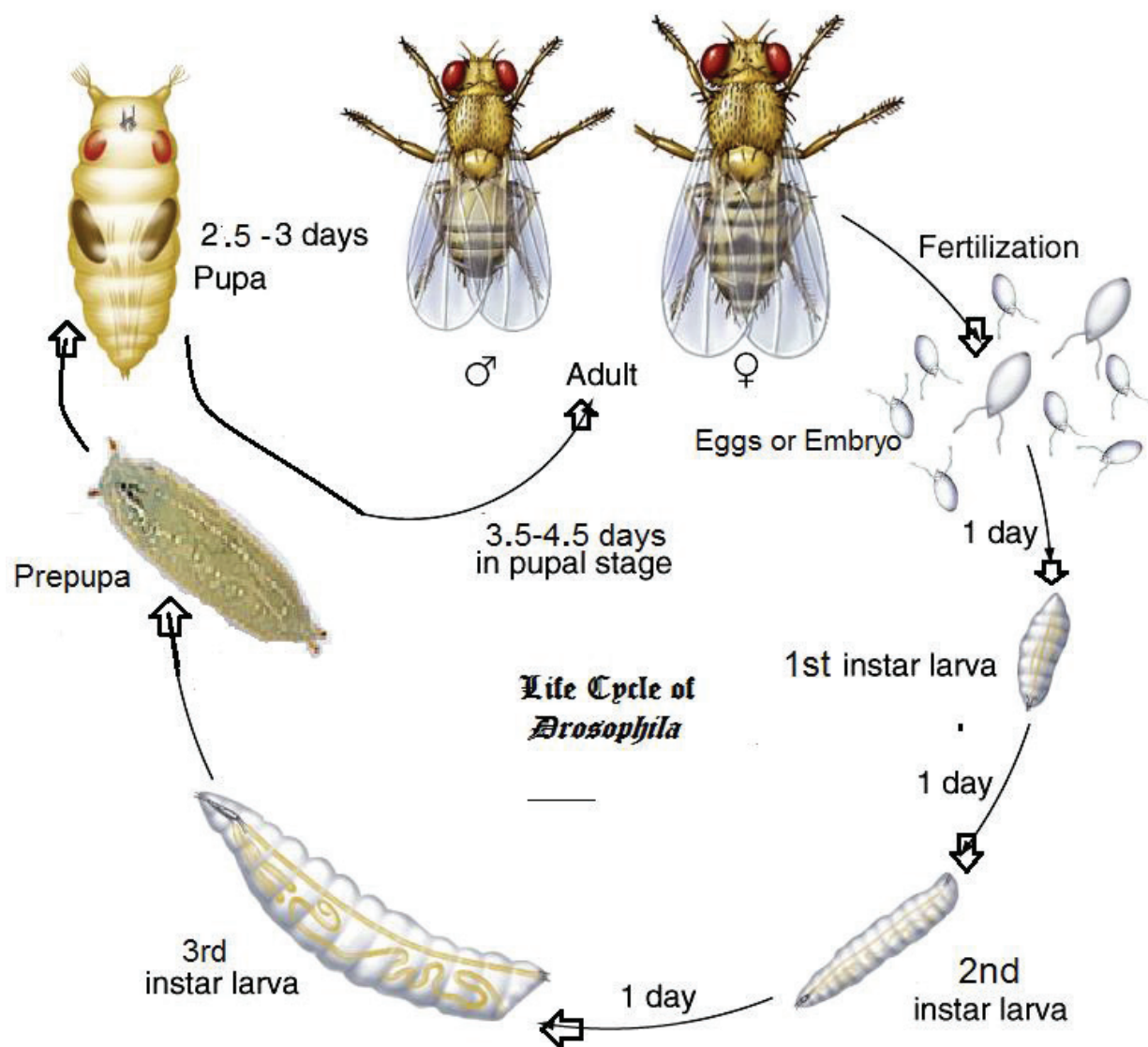
*Drosophila* contains one of the most advanced forms of eye among insects, i.e., compound eye. The unit structure of it is ommatidia; however, there are 760 ommatidia per compound eye, moreover, a cornea, eight photoreceptor cells (R1–8), many pigment cells, and some support cells are also found in each ommatidium. Reddish pigment cells are found in wild-type *Drosophila*, excess blue light is absorbed by them; therefore, ambient light is not made the fly blind [13]. As far as photoreceptor cells are concerned, they have two main parts, the rhabdomere and the cell body. However, the nucleus is an active part of the cell body, while rhabdomere is 100-µm long and consists of toothbrush-like masses of membrane, which are called microvilli. Moreover, the length and diameter (dm) of each microvillus are around 1–2 µm and 60 nm, respectively. Further, the rhodopsin is the visual protein; their approximately 100 million molecules are wrapped in rhabdomere's membrane. Accordingly, the function of rhodopsin is absorption of light. On the other hand, there are many other visual proteins that are also present in rhabdomere, which are tightly bound in the spaces among microvilli, hence, there is very little spaces for cytoplasm [14].

In *Drosophila*, there are many types of proteins that are present in photoreceptor cells, which are expressed in rhodopsin isoform, for example, blue light (480 nm) is absorbed by rhodopsin1 (Rh1), which is present in the R1–R6 photoreceptor cells. Similarly, UV light (345 and 375 nm) is absorbed by an expression of a combination of Rh3 or Rh4, which is present in the R7 and R8 photoreceptor cells. In the same way, blue (437 nm) and green (508 nm) lights are absorbed by Rh5 or Rh6, respectively. More likely, a protein opsin is also present in each photoreceptor cells, which is covalently linked to a carotenoid chromophore, i.e., 11-cis-3-hydroxyretinal. This protein is found in each rhodopsin molecule (**Figure 1c–e**) [15].

### 1.2. Lifecycle

Sexual dimorphism is characteristic of *Drosophila* spp. Therefore, males can be easily differentiated from females having differences in size and color. However, the length of female is ca. 2.5 mm, moreover, male is somewhat smaller than female with dorsal sites of male's body being darker due to a distinct black patch at the abdomen. Furthermore, in newly emerged flies and sex comb, sexual dimorphism is less noticeable (**Figure 2**) [16]. They also vary widely in their reproductive capacity. Females lay some 400 eggs (embryos), about 5 at a time, into rotting fruits or other suitable materials such as decaying mushrooms and sap fluxes. *Drosophila melanogaster*





**Figure 2.** Life-cycle of *Drosophila* (♂: male; ♀: female) with three larval instar and a pupal stages; bar on photograph: 25 cm [27].

breeds in bulky and comparatively scarce substrates. About 10–20 eggs are matured at the same time; therefore, female lays them together in one place. However, others species those oviposit only one egg in a day, breed in additional-rich but a smaller amount of nourishing resources, such as fresh leaves and grasses [17]. Eggs of *Drosophila* are ca. 0.5 mm in length, silvery, oblong, ovoid, and somewhat compressed when view laterally. Internally, an indistinguishable skinny vitelline covering warps the egg together with an exterior extracellular covering is called a chorion. At the front end, two minor respiratory filaments prolong from the dorsal surface close to the front termination; however, the tips of these extend above the surface and allow oxygen ( $O_2$ ) to reach the embryo. The anterior end can be recognized by the micropyle, a structure on the external coating surrounding the egg [18].

In usual environmental conditions, hatching of eggs takes place after 12–15 hours at 25°C (77°F) into small, white first instar maggots (larvae). Then food is taken by the resulting maggots and

their growth takes place for nearly 4 days (at 25°C). After that, they molt two times into second and third instar maggots during 24 and 48 hours after hatching, respectively. During the period of the larval stage, they are actively feed on bacteria, microbes, germs, and detritus, which are present on the rotten and decaying breeding resources that decompose the fruits, as well as on the sugar of the fruits itself, vegetable matters, and yeasts. The mother puts feces on the egg sacs to establish the same microbial composition in the larvae's guts, which works positively for them [19].

In specific conditions, their development time varies widely (between 7 and more than 60 days) between species to species and depends on the environmental factors, such as temperature, breeding substrates, and crowding. Numerous studies have shown that eggs oviposited by *Drosophila* spp. pass through an ecological cycle [20]. Nocturnally, oviposited eggs pass through favorable environmental circumstances, thus, such eggs are not vulnerable to withering from parasites [21]. Consequently, the maggots hatched from those eggs are healthy and have higher appropriateness in contrast to the maggots that are hatched from diurnal oviposited eggs. In eggs of *D. melanogaster*, a biological clock has been observed and their maggots greatly adapt to their ecological cycles, therefore, their survival becomes easy and they gain the highest benefits in their environment [22].

Then, the larvae encapsulate (pupation) in the puparium and undergo a 4-day long metamorphosis (at 25°C), after which the adults emerge [23]. The developmental period for *D. melanogaster* varies with temperature, as with many ectothermic species. They are Endopterygota, also known as Holometabola, is a superorder of insects within the infraclass Neoptera, therefore, they go through distinctive larval, pupal, and adult stages and their wings are developed internally. Duration of lifecycle of *Drosophila* spp. is variable and depends on various factors. However, it increases with the increase of temperature due to the stress of heat. Moreover, the shortest lifecycle from egg to adult, 7 days, is achieved at 28°C (82°F). Further, the same 11 days is at 30°C or 86°F. Furthermore, under the best environmental conditions, duration of lifecycle is 8.5 days at 25°C (77°F), under moderate conditions, 19 days is at 18°C (64°F), under low conditions, it takes over 50 days at 12°C (54°F) [23]. While under crowded condition, lifecycle is prolonged with emergence of smaller flies. However, their average life span is 35–45 days. (Figure 2; Table 2) [6].

S. no	LC in d	Temperatures		Type of life cycle
		°C	°F	
1.	7	28	82	Shortest life cycle
2.	8.5	25	77	Under ideal conditions
3.	11	30	86	–
4.	19	18	64	–
5.	50	12	54	Longest life cycle
6.	35–45	15–35	59–95	Average life cycle

LC, life cycle of *Drosophila* spp.; d, days; °C, degree celsius; °F, fahrenheit.

**Table 2.** Duration of life cycle of *Drosophila* spp. on different temperatures.

According to the studies of living organisms related to sperm, the longest sperm cells, i.e., 58 mm (2.3 in) in length, are found in males of *Drosophila bifurca* compared to any animal that exists on this universe [24]. Structurally, sperms consist of a head with nucleus and a long tail with tangled coils. Other species of genus *Drosophila* also form somewhat gigantic sperm cells; however, the longest sperms are produced by *D. bifurca* [19]. The length of the sperm cells of *D. melanogaster* is 1.8 mm, which has an adequate length, while, a human sperm is still around 35 times shorter than *D. bifurca*'s sperm. A number of *Drosophila* spp. are known to mate by traumatic insemination [25]. In *Drosophila* female, sperm are stored in a tubular and two mushroom-shaped receptacle structures, which are called spermathecae. In polyandrous female, strong sperm competition takes place for fertilization of eggs. It is observed that the sperm precedence of last male mated is utilized for production of descendent. The female sires about 80% of her offspring with the sperm inseminated by the previous male to mate. Both displacement and incapacitation are responsible for this precedence [26].

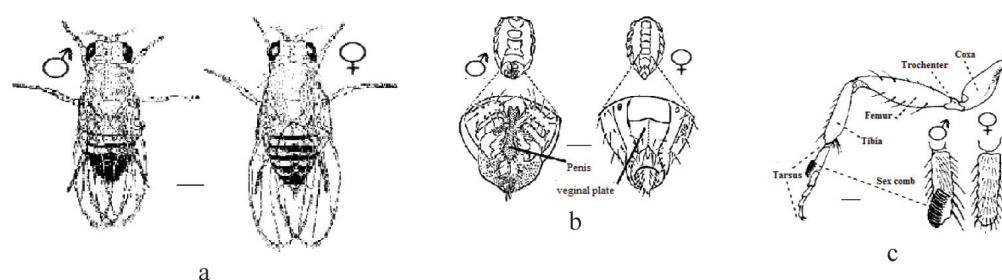
## 2. *Drosophila* genetics

*Drosophila* was the first organisms to be studied genetically; perhaps it is the best understood animal in genetic systems. It has a small size, short lifecycle, high reproductive rate, easy to culture, and easy genetic manipulation. It is one of the most valuable organisms in biology, developmental biology, genetics, medicine, human disease, and stem cell research. One species of *Drosophila* in particular, *D. melanogaster*, has been comprehensively used in genetics as a common model and toolbox organism in modern biology. People have been working on it, since ancient time, consequently, very much is already known about it, therefore, it is easy to handle and well understood. It is cheap and easy to keep in large numbers. From the past century as well as at present, *Drosophila* has been used for advancement in learning, studies, education, and research. Many different aspects of *Drosophila* have been studied by thousands of scientists. Its significance for human health was documented by the award of the Nobel Prize in medicine/physiology to Lewis, Volhard and Wieschaus in 1995 [28].

### 2.1. Sex distinguish

In *Drosophila*, female's abdomen consists of seven segments with many dark transverse stripes and pointed tip. However, male's abdomen consists of five segments with two dark stripes and more curved with heavily pigmented tip. Moreover, in a newly immersed adult male, the pigmentation is not observed. Further, the gender of *Drosophila* can be differentiated by the structure of the external genitalia and their color. Furthermore, the abdomen is pale and relatively smooth in mature female, in comparison with dark genitalia that are found in mature male. Additionally, a secondary sexual character is also present in the male flies, which is called sex comb, a structure that consists of a minor cluster of about 10 black hairs in front of the last large segment (third segment counting from the end of the body). The same is also present even in immature males. Likewise, another secondary sexual character in male, the presence of a cluster of spiky hairs (claspers) surrounding the reproducing parts used to attach to the female during mating (**Figure 3**) [16].





**Figure 3.** Dorsal view of male (left) and female (right) *Drosophila*: five segments and rounded abdomen in male and seven segments and pointed abdomen in female (a); ventral view of genitalia of male (left) and female (right) (b); left foreleg of male with sex comb on tarsus of male fly (left) and female sex comb absent in female fly (c); drawn by W. Hewitt; bar on photograph: 25 cm.

## 2.2. Virgin females

All female flies, which are used in genetic experiments for making control crosses, should be virgin. As a concern, after 8 hours of emerging from pupal stage, *Drosophila* females are able to mate with males. Likewise, they are capable of mating with many or multiple males; therefore, they are called as polyandrous. On the other hand, when they mate, males inseminate millions of viable sperms, which are stored in spermathecae of females for several days and this will puzzle the outcomes of a following orderly mating. Therefore, to prevent multiple mating, all adult *Drosophila*, specially, females are isolated 7 hours earlier to utilize them for experiment, consequently, that all freshly produced *Drosophila* will remain virgin [29].

## 2.3. Sex chromosomes

Different organisms have diverse sex determination mechanisms. Mostly, females are defined as homogametic (all gametes will carry the X chromosome: XX); however, males are known as heterogametic (half the gametes carry the X and half the Y chromosome: XY). The examples of the same are species such as humans and *Drosophila*, etc. The genes carried on the X chromosome and those carried on the Y chromosome, consequently, distinction has made between them. Since sex chromosomes as well as autosomes have been correlated the law of segregation. The genes on the X chromosome are distributed independently from genes on the Y chromosome (Figure 4) [28].



**Figure 4.** Metaphase chromosomes from dividing cells of larval ganglion (brain) of *Drosophila melanogaster*: chromosomes of female (a) consist of three pairs of autosomes and one pair of rod-shaped X chromosomes; chromosomes of male (b) consist of three pairs of autosomes, one X chromosome, and one Y chromosome; bar on photograph: 10  $\mu\text{m}$  [30].

## 2.4. *Drosophila* as model systems

The boundaries of human genetics, however, sort it essential to practice prototypical systems to evaluate precious genes and passageways in more detail. During the past 20 years, investigation utilizing the genetically acquiescent fruit fly has known *D. melanogaster* as an appreciated model system in the learning of human neurodegeneration. These studies offer reliable models for Parkinson's, motor neuron, and Alzheimer's diseases, as well as models for trinucleotide repeat expansion diseases, including Huntington's and ataxias disease. As a consequence of these studies, many signaling pathways comprising target of rapamycin (TOR), c-Jun N-terminal kinase (JNK), bone morphogenetic protein (BMP) signaling, and phosphatidylinositol 3-kinase (PI3K)/Akt have been revealed to be decontrolled in models of proteinopathies suggesting that two or more starting actions may activate disease formation in an age-related manner [31]. Moreover, these studies also determine that *Drosophila* can be utilized to monitor chemical compounds for their prospective to inhibit or enhance the disease, which in order can openly monitor medical research and the expansion of original therapeutic approaches for handling of human neurodegenerative diseases. Human neurodegenerative diseases are demoralizing illnesses that principally disturb aging individuals. The bulk of the ailments are related with pathogenic oligomers from misfolded proteins, ultimately producing the development of masses and the advanced damage of neurons in the brain and central nervous system (CNS). Many of these proteinopathies are sporadic and the source of pathogenesis leftovers obscure. Inborn forms are linked with genetic deficiencies, suggesting that the affected protein is causally related to diseases formation and/or progression [32, 33].

## 3. Summary

*Drosophila* belongs to the family Drosophilidae, whose members are most frequently called the fruit flies. Since ancient time, *Drosophila* is used as a model and toolbox for biology, genetics, medicine, human disease, and stem cell research. It was nearly 100 years ago that Thomas H. Morgan reported the identification of the white gene in *Drosophila melanogaster*. Genetic approaches dominated the first 50 years of research in *Drosophila* (1910–1960), concentrating on dissecting the principles of inheritance. In this period, important concepts and tools were developed that allowed the study of many other biological processes during 1960–2010. Certainly, investigators realized in the early 1950s that genetic approaches could be used to study problems other than heredity. The uninterrupted development of research tools during 1960–2010 has driven numerous new discoveries in *Drosophila*. This is an appropriate time to reflect on the past and present contributions of *Drosophila* research in different fields, and therefore, the present book on “*Drosophila*” aims to publish this. *Drosophila* offers many unique advantages that will ensure that it is a premier research organism since ancient time to recent to future and for every field of research. After 100 years, fruit flies continue to be the choice model system for many neuroscientists. Example of recent contribution of research in *Drosophila* relates to numerous aspects of the physiological properties of sleep that is shared between *Drosophila* spp. and humans. Another example relates to Parkinson's disease. The work on parkin and PINK1 mutation, *D. melanogaster* has provided evidence that regulating mitochondrial remodeling and dysfunction is a

cause of Parkinson's disease. Recently, many *Drosophila* experts have focused their attention on dissecting the molecular and cellular basis of the behavior. These include phototaxis, chemotaxis, aggression, physical response to mechanical stimuli, escape behavior, and sex. These studies will undoubtedly advance our understanding of how the nervous system of *Drosophila* works and provide us with very valuable paradigms to study mammalian brain function. This book provides window for *Drosophila* research as a toolbox for biology and medicine and its profile acts in top creatures for science experimentation. *Drosophila*'s contribution to ageing, basal body, stem cell, nanoparticles, and artificial intelligence research is helping us to open new doors of research. A fluorescent tagging approach can be used in *Drosophila* to pest and vector risk assessment. Cloning and characterization in *Drosophila* can be exposed novel entries in the future of *Drosophila*. This book aims to provide the readers with a comprehensive overview on the historical, modern, and future prospects on this important insect, *Drosophila*, featuring an easy-to-follow, vignette-based format that will be focusing on the most important research-oriented evidences on various advantageous aspects for parasitologists, entomologists, neurologists, evolutionists, researchers, scientists, students, and others.

## Author details

Farzana Khan Perveen

Address all correspondence to: farzana\_san@hotmail.com

Department of Zoology, Shaheed Benazir Bhutto University (SBBU), Main Campus, Sheringal, Khyber Pakhtunkhwa (KP), Pakistan

## References

- [1] Green MM. It really is not a fruit fly. *Genetics*. 2002;**162**:1-3
- [2] Beers EH, Smith TJ, Walsh DB. Spotted wing drosophila, *Drosophila Suzukii* (Matsumura) (Diptera: Drosophilida). *Orchard Pest Management*. 2010;47-39. Online: <http://jenny.tfrec.wsu.edu/opm/displaySpecies.php?pn=165> (Accessed: 29/4/2011)
- [3] Patterson C. *Evolution*. Cornell University Press, Cornell, United State of America (USA). 1999;45-55
- [4] Markow TA, O'Grady PM. *Drosophila: A guide to species identification and use*. Elsevier, London, United Kingdom (UK). 2005;56-76
- [5] Brake I, Bächli G. Drosophilidae (Diptera). *World Catalogue of Insects*. 2008;1-412
- [6] O'Grady P, DeSalle R. Out of Hawaii: the origin and biogeography of the genus *Scaptomyza* (Diptera: Drosophilidae). *Biology Letters*. 2008;**4**(2):195-199. DOI: 10.1098/rsbl.2007.0575

- [7] Castrezana S. New records of *Zaprionus indianus* Gupta, 1970 (Diptera: Drosophilidae) in North America and a key to identify some *Zaprionus* species deposited in the *Drosophila* Tucson Stock Center. *Drosophila Information Service*. 2007;**90**:34-36
- [8] Linde KVD, Steck GJ, Hibbard K, Birdsley JS, Alonso LM, Houle D. First records of *Zaprionus indianus* (Diptera: Drosophilidae), a pest species on commercial fruits, from Panama and the United States of America. *Florida Entomologist*. 2006;**89**(3):402-404. DOI: 10.1653/0015-4040(2006)89[402:FROZID]2.0.CO;2
- [9] Online. Fly (Fruit) *Drosophila melanogaster*. Taranaki Educational Resource: Research, Analysis and Information Network (TER: RAIN); 2016. Online: <http://www.terrain.net.nz/friends-of-te-henui-group/local-flies/common-fruit-fly-drosophila-melanogaster.html> (Accessed: 23/11/2016)
- [10] Carreira VP, Soto IM, Mensch J, Fanara JJ. Genetic basis of wing morphogenesis in *Drosophila*: sexual dimorphism and non-allometric effects of shape variation. *BMC Developmental Biology*. 2011;**11**:32. DOI: 10.1186/1471-213X-11-32
- [11] Vilela CR. Is *Zaprionus indianus* Gupta, 1970 (Diptera: Drosophilidae) currently colonizing the Neotropical region? *Drosophila Information Service*. 1999;**82**:37-39
- [12] Fry S, Dickinson M. The aerodynamics of free-flight maneuvers in *Drosophila* (PDF). *Science*. 2003;**300**(5618):495-498. DOI: 10.1126/science.1081944
- [13] Hardie RC, Raghu P. Visual transduction in *Drosophila*. *Nature*. 2001;**413**(6852):186-93. DOI: 10.1038/35093002
- [14] Raghu P, Colley NJ, Webel R, et al. Normal photo transduction in *Drosophila* photoreceptors lacking an InsP(3) receptor gene. *Molecular and Cellular Neuroscience*. 2000;**15**(5):429-45. DOI: 10.1006/mcne.2000.0846
- [15] Wang T, Xu H, Oberwinkler J, Gu Y, Hardie R, Montell C, et al. Light activation, adaptation and cell survival functions of the Na<sup>+</sup>/Ca<sup>2+</sup> exchanger CalX. *Neuron*. 2005;**45**(3):367-378. DOI: 10.1016/j.neuron.2004.12.046
- [16] Chiang HC, Hodson AC. An analytical study of population growth in *Drosophila melanogaster*. *Ecological Monographs*. 1950;**20**(3):173-206. DOI: 10.2307/1948580
- [17] Bakker K. An analysis of factors which determine success in competition for food among larvae of *Drosophila melanogaster*. *Archives Neerlandaises de Zoologie*. 1961;**14**(2):200-281. DOI: 10.1163/036551661X00061
- [18] Broughton SJ, Piper MD, Ikeya T, Bass TM, Jacobson J, Driege Y, Martinez P, Hafen E, Withers DJ, Leivers SJ, Partridge L. Longer lifespan, altered metabolism, and stress resistance in *Drosophila* from ablation of cells making insulin-like ligands. *Proceedings of the National Academy of Sciences of the United States of America*. 2005;**102**(8):3105-3110. DOI: 10.1073/pnas.0405775102
- [19] Pitnick S, Spicer GS, Therese A, Markow A. How long is a giant sperm? *Nature*. 1995;**375**(6527):109. DOI: 10.1038/375109a0



- [20] Markow TA, O'Grady PM. *Drosophila*: a guide to species identification and use. Elsevier Publisher, London, United Kingdom (UK). 2005;34-49
- [21] Remsen J, O'Grady P. Phylogeny of Drosophilinae (Diptera: Drosophilidae), with comments on combined analysis and character support. *Molecular Phylogenetics and Evolution*. 2002;4(2):249-264. DOI: 10.1016/S1055-7903(02)00226-9
- [22] Patterson C. *Evolution*. Cornell University Press, New York (NY), United State of America (USA). 1999;1-70
- [23] Ashburner M, Thompson JN. The laboratory culture of *Drosophila*. In: Ashburner M, Wright TRF (eds). *The Genetics and Biology of Drosophila*. Academic Press, Georgia, United State of America. 1978;2A:1-81
- [24] Joly D, Luck N, Dejonghe B. Adaptation to long sperm in *Drosophila*: correlated development of the sperm roller and sperm packaging. *Journal of Experimental Zoology B: Molecular and Developmental Evolution*. 2007;310B(2):167-178. DOI: 10.1002/jez.b.2167
- [25] Howlader G, Sharma KV. Circadian regulation of egg-laying behavior in fruit flies *Drosophila melanogaster*. *Journal of Insect Physiology*. 2006;52:779-785
- [26] Pitnick S. Investment in testes and the cost of making long sperm in *Drosophila*. *American Naturalist*. 1996;148:57-80. DOI: 10.1086/285911
- [27] Weigmann K, Klapper R, Strasser T, Rickert C, Technau G, Jäckle H, Janning W, Klämbt C. FlyMove: a new way to look at development of *Drosophila*. *Trends in Genetics*. 2003;19(6):310-311. DOI: 10.1016/S0168-9525(03)00050-7
- [28] Wolf MJ, Rockman HA. *Drosophila melanogaster* as a model system for genetics of post-natal cardiac function. *Drug Discovery Today Diseases Models*. 2008;5(3):117-123. DOI: 10.1016/j.ddmod.2009.02.002
- [29] Sokolowski MB. *Drosophila*: genetics meets behaviour. *Nature Review Genetics*. 2001;2(11):879-890. DOI: 10.1038/35098592
- [30] Demerece M, Kaufmann BP. *Drosophila* Guide. 10th Edition; Carnegie Institute of Washington DC, United State of America (USA). 1996;1-46
- [31] Kamimura Y. Twin intermittent organs of *Drosophila* for traumatic insemination. *Biology Letters, The Royal Society, London, United Kingdom (UK)*. 2007;3(4):401-404. DOI: 10.1098/rsbl.2007.0192
- [32] Catherine P, Kelly D, Jerry C. Sperm competition between *Drosophila* males involves both displacement and incapacitation. *Nature*. 1999;400(6743):449-452. DOI: 10.1038/22755
- [33] Hirth F. *Drosophila melanogaster* in the study of human neurodegeneration. *CNS and Neurological Disorders Drug Targets*. 2010;9(4):504-523. DOI: 10.2174/187152710791556104