Genetics in animal models; *Drosophila melanogaster*, mice ..

Liam Keegan,

Liam.Keegan@ceitec.muni.cz

CEITEC A35, Rm 143

Syllabus:

- 1. History: After Mendel rediscovery; beginnings of *Drosophila* and rodent genetics. Life cycles, breeding and genetic methods for *Drosophila* and mice. Visible mutant markers

- 2. *Drosophila* Balancer chromosomes; Bar eye, Curly wings and Stubble bristle dominant balancer markers and other markers. Genetic screens in flies, mice and zebrafish

- 3. *Drosophila* embryonic development and metamorphosis; The Wieschaus, Nusslein-Vollhard genetic screen for larval segmentation and patterning mutants

- 4. Other important genetic screens for Drosophila developmental mutants; screens in Daniel St Johnston review.

- 5. Selected topics in fly and mouse genetics; Homeotic genes, planar cell polarity and organ specification in flies, mice and zebrafish
- 6. Growth control, cancer and cell death in flies, mice and fish
- 7. Innate immunity in flies, mice and fish. Ageing.
- 8. Genetic control of nervous system development in Drosophila, specification of neuronal cell types, motorneuron specification and coordination in flies, mice and fish
- 9. Genetic control of development in sensory systems, vision, olfaction in flies, mice and fish
- 10. Genetic investigations of learning, memory, forgetting in flies, mice and fish
- 11. Genetic investigations of specific behaviours; circadian rhythms, sleep, mating etc. in flies, mice and fish
- 12. Other model systems, with invited lecturers; C. elegans, Killifish, other rodents maybe
- 13. Other model systems, with invited lecturers; C. elegans maybe, Killifish, other rodents
- 14. Other model systems, with invited lecturers; C. elegans maybe, Killifish, other rodents
- Literature:

Introduction to *Drosophila*

- Bing Videos

Go to FlyBase.org
FlyBase Homepage for introductory information

- FlyBase is maintained at Cambridge, UK and Berkeley, California
- Curators read new fly papers and update information on fly genes
- Collect information on new fly strains

- Go to New to flies? page
- Go to Fly Basics page and find links to papers on the next slide

Primers on *Drosophila* genetics

- **Genetics** on the **Fly**: A Primer on the *Drosophila* Model System
- KG Hales, CA Korey, AM Larracuente, DM Roberts - **Genetics**, 2015 - academic.oup.com
- Read first half of this. Also history and glossary at the end

- The **joy** of **balancers**
- DE Miller, KR Cook, RS Hawley - PLoS genetics, 2019 - journals.plos.org
- Short. Read all of it

- How to Design a Genetic Mating Scheme: A Basic Training Package for *Drosophila* Genetics
- J **Roote**, A **Prokop** - G3: Genes| Genomes| Genetics, 2013 - academic.oup.com
- Look at supplementary files and read early parts. Gets too complicated later.

Genetics on the Fly: A Primer on the *Drosophila* Model System

Karen G. Hales,*,[1] Christopher A. Korey,[†] Amanda M. Larracuente,[‡] and David M. Roberts[§]
*Department of Biology, Davidson College, Davidson North Carolina 28035, [†]Biology Department, College of Charleston, Charleston, South Carolina 29424, [‡]Department of Biology, University of Rochester, Rochester, New York 14627, and [§]Biology Department, Franklin and Marshall College, Lancaster, Pennsylvania 17604

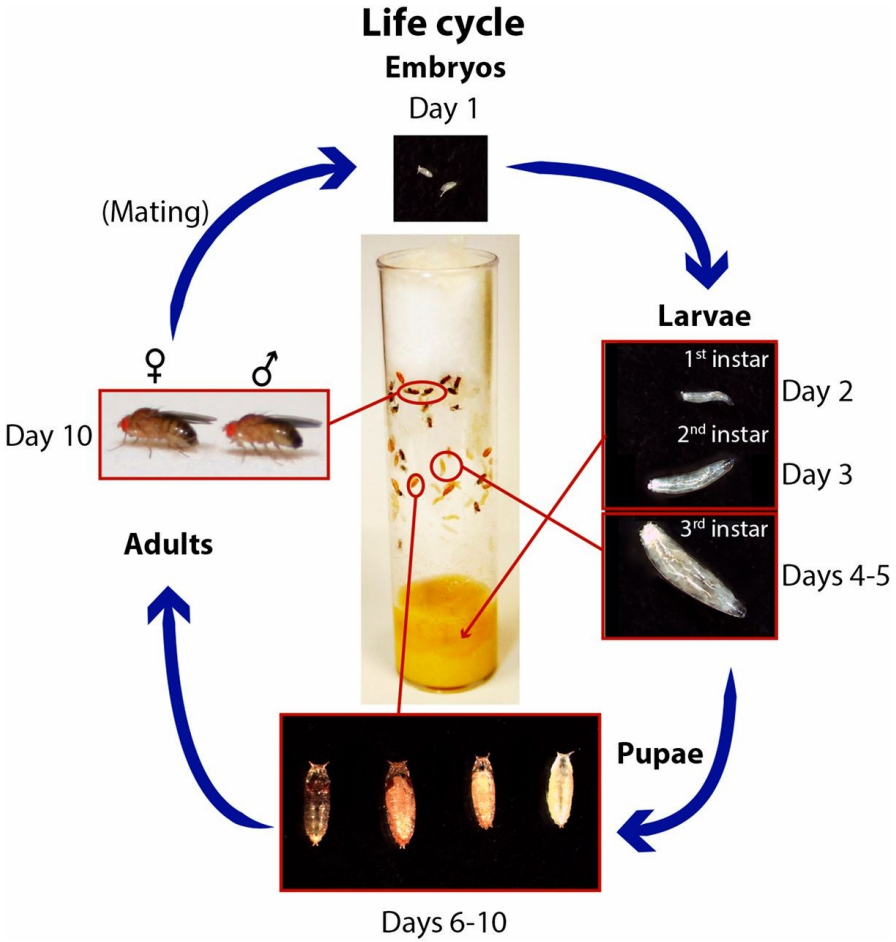
ABSTRACT Fruit flies of the genus *Drosophila* have been an attractive and effective genetic model organism since Thomas Hunt Morgan and colleagues made seminal discoveries with them a century ago. Work with *Drosophila* has enabled dramatic advances in cell and developmental biology, neurobiology and behavior, molecular biology, evolutionary and population genetics, and other fields. With more tissue types and observable behaviors than in other short-generation model organisms, and with vast genome data available for many species within the genus, the fly's tractable complexity will continue to enable exciting opportunities to explore mechanisms of complex developmental programs, behaviors, and broader evolutionary questions. This primer describes the organism's natural history, the features of sequenced genomes within the genus, the wide range of available genetic tools and online resources, the types of biological questions *Drosophila* can help address, and historical milestones.

KEYWORDS *Drosophila*; development; comparative genomics; model organism;

TABLE OF CONTENTS

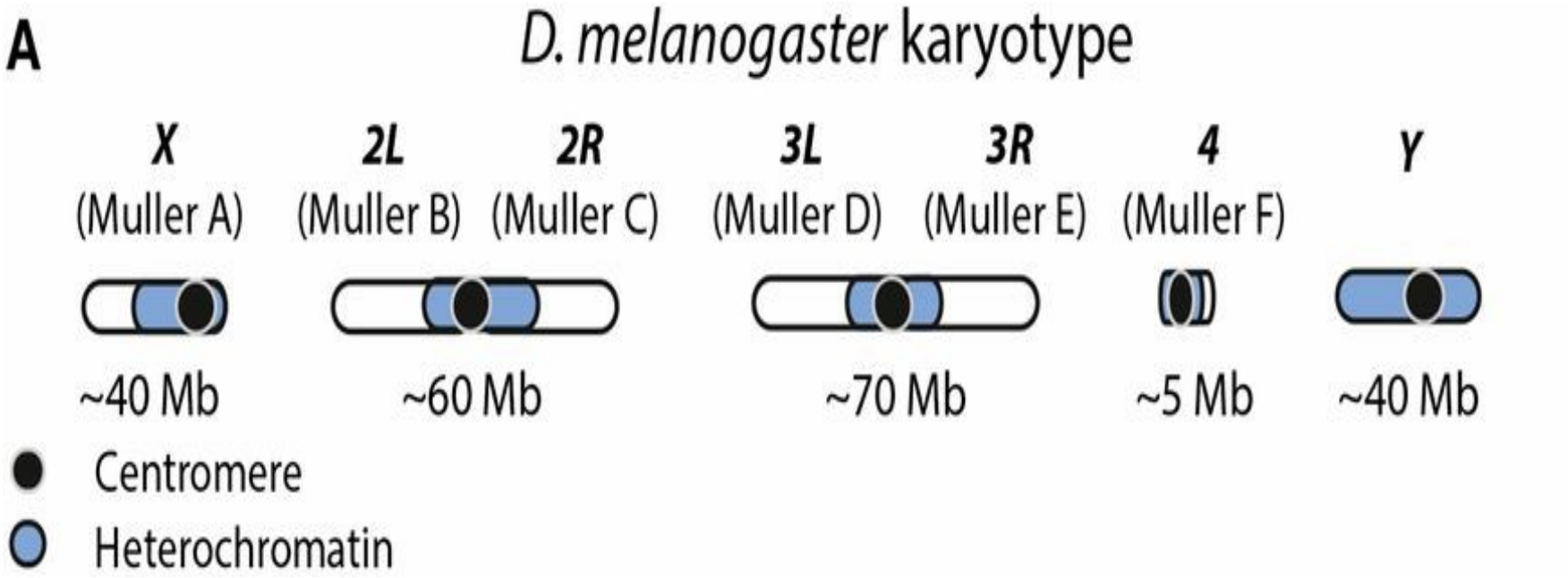
Continued

Figure 1 Life cycle of *D. melanogaster*. *D. melanogaster* are cultured in vials with food in the bottom and a cotton, ...

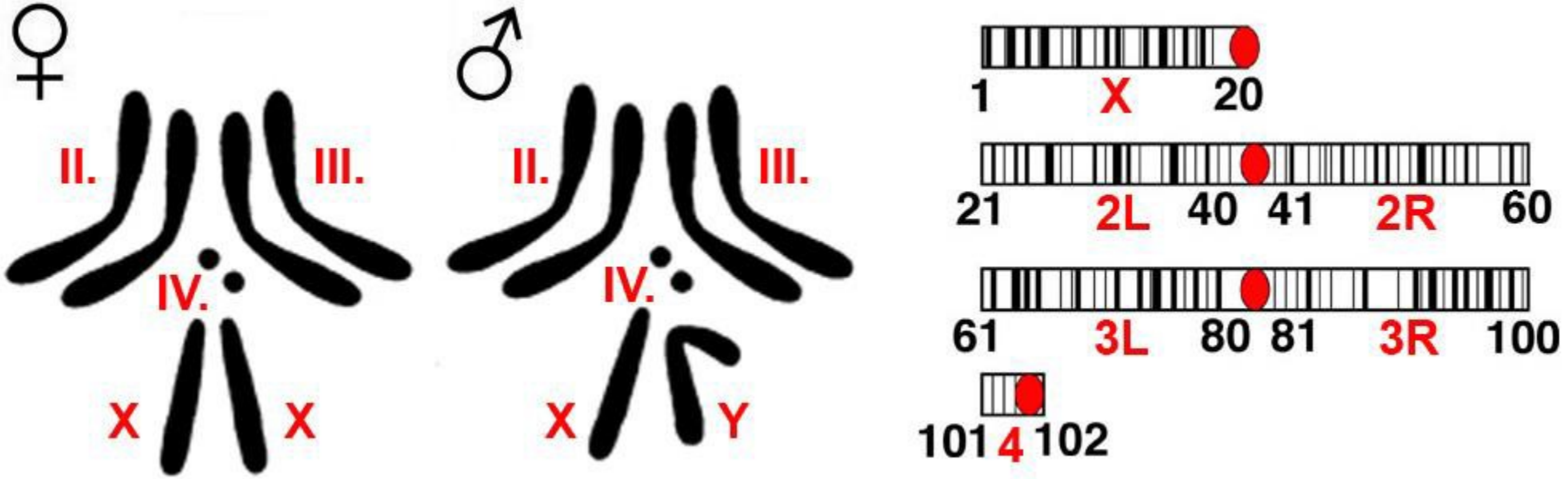


Genetics, Volume 201, Issue 3, 1 November 2015, Pages 815–842, https://doi.org/10.1534/genetics.115.183392

Figure 3 Genome organization and phylogeny. (A) Organization of the Drosophila melanogaster genome. D. melanogaster ...



Genetics, Volume 201, Issue 3, 1 November 2015, Pages 815–842, https://doi.org/10.1534/genetics.115.183392



- **Figure 5.** *Drosophila* chromosomes
- Cytological images of mitotic *Drosophila* chromosomes.
- **Left**: Female and male cells contain pairs of heterosomes (X, Y) and three autosomal chromosomes.
- **Right**: Schematic illustration of *Drosophila* salivary gland polytene chromosomes which display a reproducible banding pattern which can be used for the cytogenetic mapping of gene loci (black numbers); 2nd and 3rd chromosomes are subdivided into a left (L) and right (R) arm, divided by the centrosome (red dot). Detailed descriptions of *Drosophila* chromosomes can be found elsewhere [52].

How to Design a Genetic Mating Scheme: A Basic Training Package for *Drosophila* Genetics

John Roote* and Andreas Prokop†,1
*Department of Genetics, University of Cambridge, Cambridge CB2 3EH, United Kingdom, and †Faculty of Life Sciences, University of Manchester, Manchester M13 9PT, United Kingdom

ABSTRACT *Drosophila melanogaster* is a powerful model organism for biological research. The essential and common instrument of fly research is genetics, the art of applying Mendelian rules in the specific context of *Drosophila* with its unique classical genetic tools and the breadth of modern genetic tools and strategies brought in by molecular biology, transgenic technologies and the use of recombinases. Training newcomers to fly genetics is a complex and time-consuming task but too important to be left to chance. Surprisingly, suitable training resources for beginners currently are not available. Here we provide a training package for basic *Drosophila* genetics, designed to ensure that basic knowledge on all key areas is covered while reducing the time invested by trainers. First, a manual introduces to fly history, rationale for mating schemes, fly handling, Mendelian rules in fly, markers and balancers, mating scheme design, and transgenic technologies. Its self-study is followed by a practical training session on gender and marker selection, introducing real flies under the dissecting microscope. Next, through self-study of a PowerPoint presentation, trainees are guided step-by-step through a mating scheme. Finally, to consolidate knowledge, trainees are asked to design similar mating schemes reflecting routine tasks in a fly laboratory. This exercise requires individual feedback but also provides unique opportunities for trainers to spot weaknesses and strengths of each trainee and take remedial action. This training package is being successfully applied at the Manchester fly facility and may serve as a model for further training resources covering other aspects of fly research.

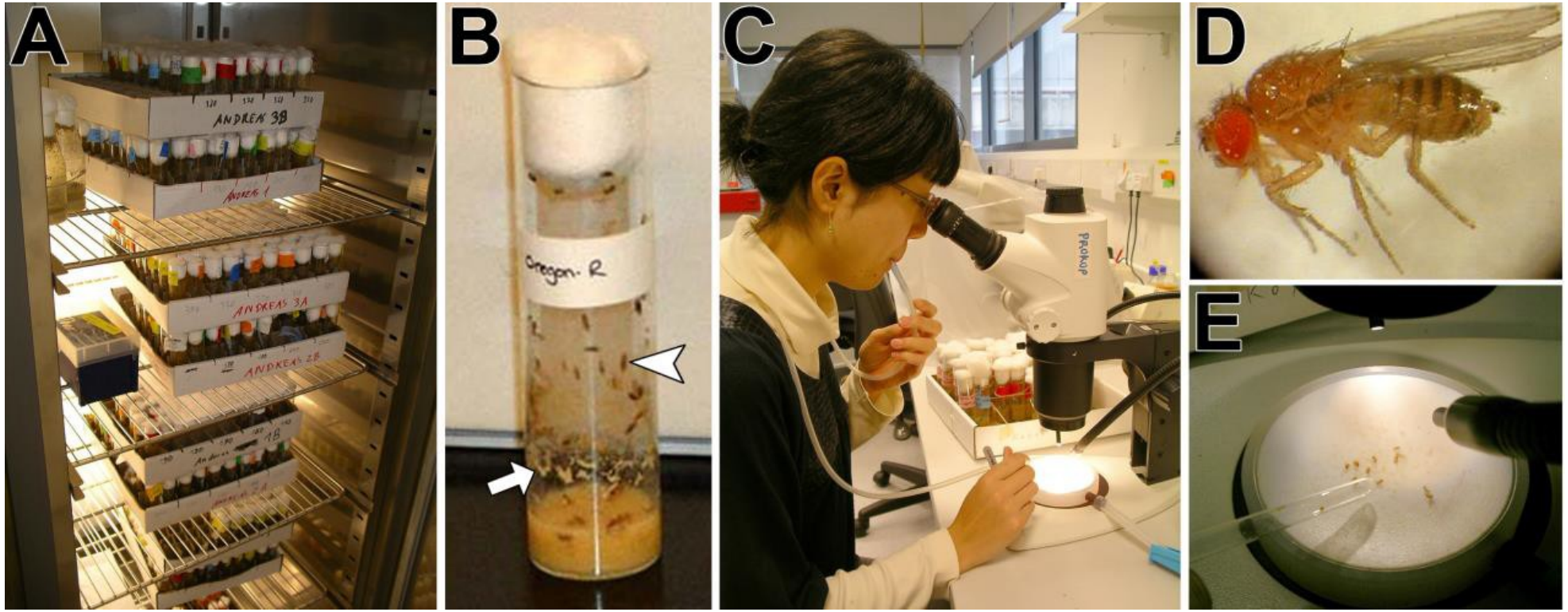
KEYWORDS
Drosophila
classical genetics
transgenesis
education
model organism

For a century, the fruit fly *Drosophila* has been used as a powerful model organism for biological research (Ashburner 1993; Bellen *et al.* 2010; Martinez Arias 2008). Initially the fly was the essential vehicle for classical genetics until the basic genetic rules and tools generated during the first half of the 20th century were recognized and used as a powerful means to dissect biological problems (Keller 1996). For the last 50 years, fly genetics has been systematically and successfully applied to decipher principle mechanisms underpinning numerous fundamental biological processes, including development (Lawrence 1992), signaling (Cadigan and Peifer 2009), cell cycle (Lee and Orr-Weaver 2003), nervous system development, function and behavior (Bellen *et al.* 2010; Weiner 1999), and even the molecular aspects of human disease (Bier 2005). Given the high degree of evolutionary conservation, this work has laid important foundations for research in mammals (Bellen *et al.* 2010), and the fly continues to play this role. Its future importance is obvious, for example, when considering the increasing amounts of human disease genes that are being discovered, for many of which the principal biological functions still need to be unraveled.

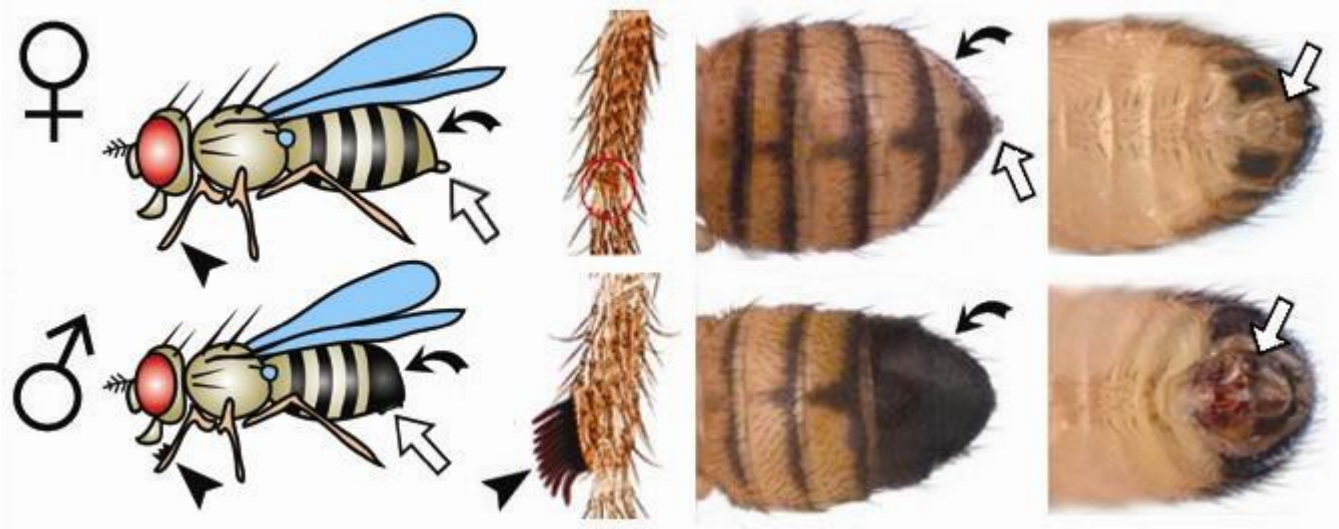
To carry out such work, classical genetic tools and rules still have a pivotal place in current *Drosophila* research. In addition, fly genetics has been further revolutionized through the advent of molecular biology, the sequencing of the fly genome, the discovery of transposable elements as a vehicle for transgenesis, targeted gene expression systems, the systematic generation of deletions, transposable element insertions and transgenic knock-down constructs covering virtually every *Drosophila* gene, as well as the application of recombinases or target-specific nucleases to perform genomic engineering (Dahmann 2008; Venken and Bellen 2005).

doi: 10.1534/g3.112.004820
Manuscript received October 28, 2012; accepted for publication December 18, 2012

Supporting information is available online at http://figshare.com/articles/



- **Figure 3.** Maintaining and handling flies in the laboratory
- **A)** Fly stocks are stored in large numbers on trays in temperature controlled rooms/incubators1 (the trays shown here each hold two copies of 50 stocks).
- **B)** Each fly stock is kept in glass or plastic vials which contain food at the bottom and are closed with foam, cellulose acetate, paper plugs or cotton wool. Larvae live in the food and, at the wandering stage, climb up the walls (white arrow) where they subsequently pupariate (white arrow head).
- **C-E)** To score for genetic markers and select virgins and males of the desired phenotypes, flies are immobilised on CO_2-dispensing porous pads (E), visualised under a dissecting scope (C, D) and then discarded into a morgue or transferred to fresh vials via a paint brush, forceps or pooter / aspirator 2 (C, E). For further information on how a typical fly laboratory is organised see other sources [3,4,5,102] 3.



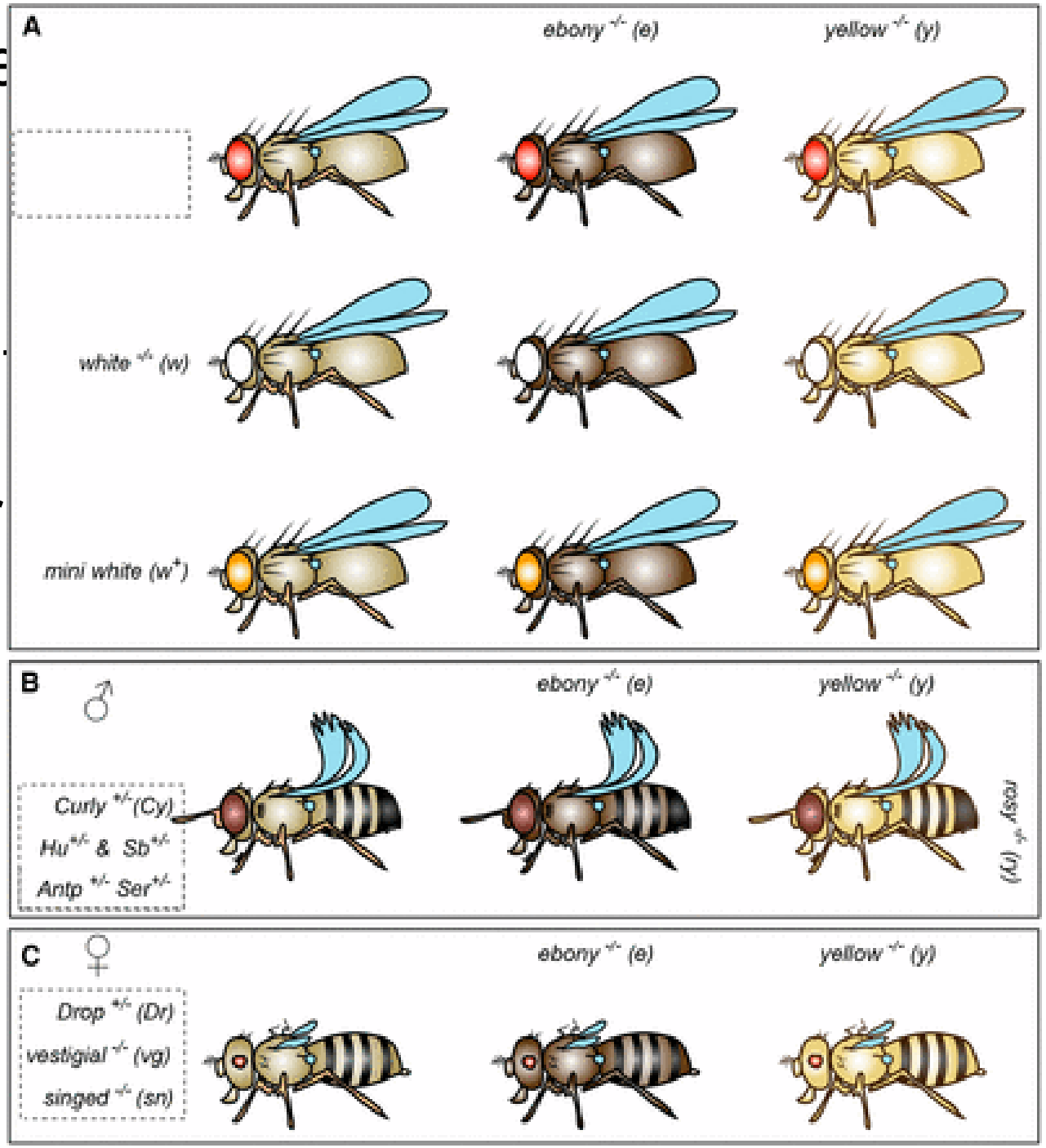
- **Figure 4.** Criteria for gender selection
- Images show females (top) and males (bottom): lateral whole body view (1st column), a magnified view of the front legs (2nd column), dorsal view (3rd column) and ventral view (4th column) of the abdomen.
- Only males display sex combs on the first pair of legs (black arrow heads). Females are slightly larger and display dark separated stripes at the posterior tip of their abdomen, which are merged in males (curved arrows). Anal plates (white arrows) are darker and more complex in males and display a pin-like extension in females. The abdomen and anal plate are still pale in freshly eclosed males and can be mistaken as female indicators at first sight. Photos are modified from [1] and [29].
- During a very short period after eclosion, flies display a visible dark greenish spot in their abdomen (*meconium*; not shown) which can be taken as a secure indicator of female virginity even if fertile males are present.

Commonly –used visible markers to follow chromosomes through crosses;

Dominant mutant (Capi letter) and

recessive mutant (lower case letter.)

Mouse mutants have to be genotyped by PCR.



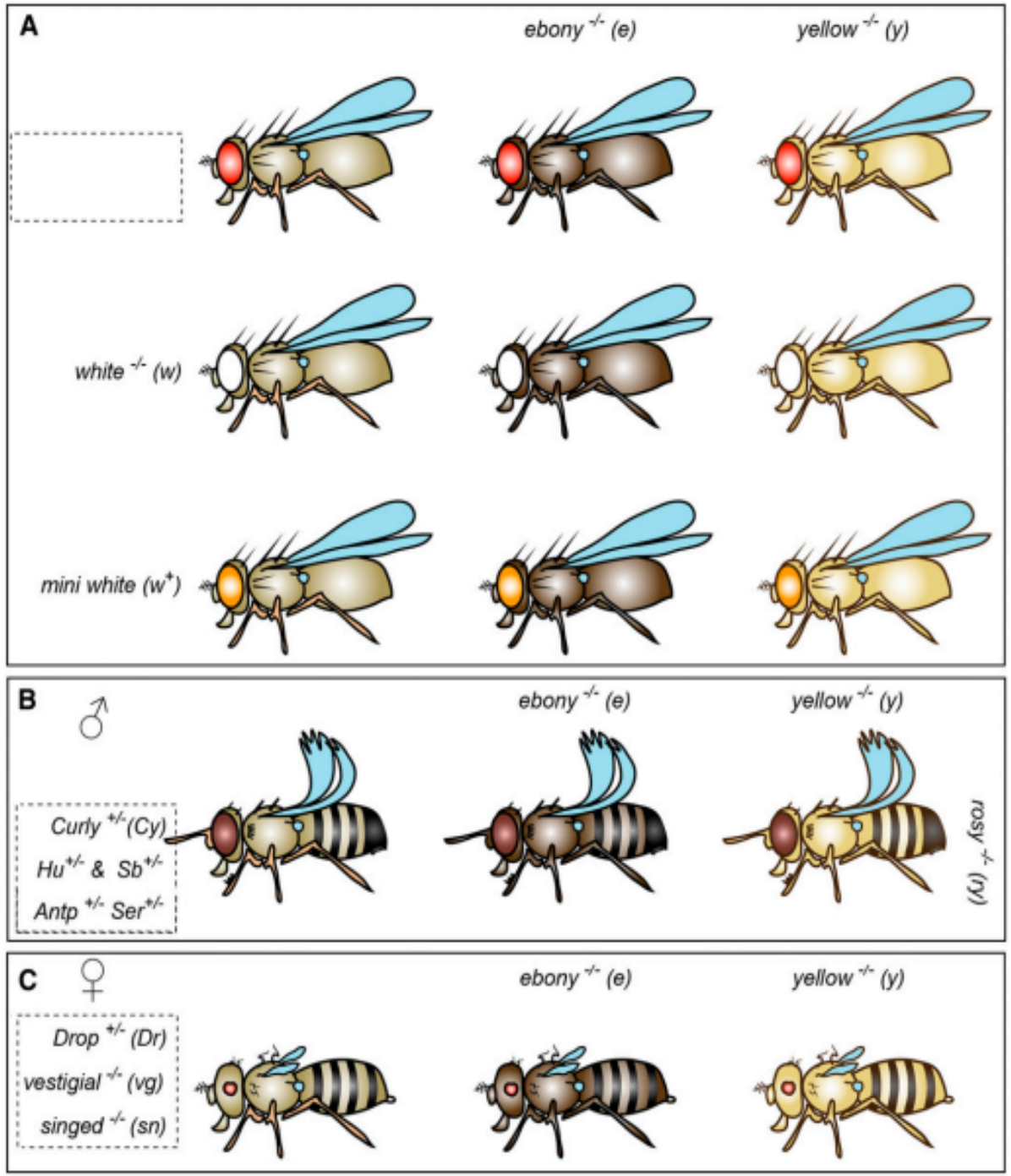
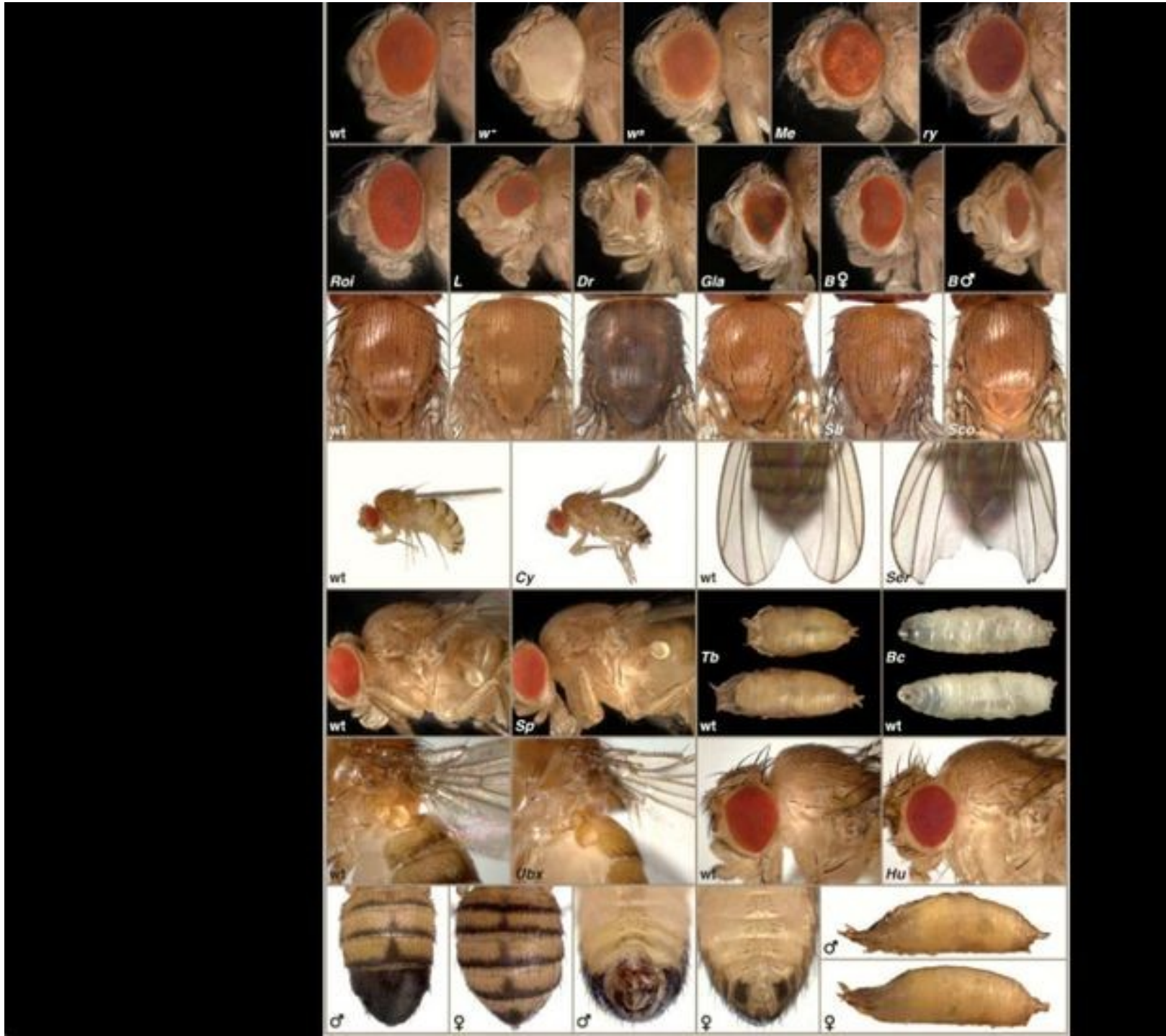


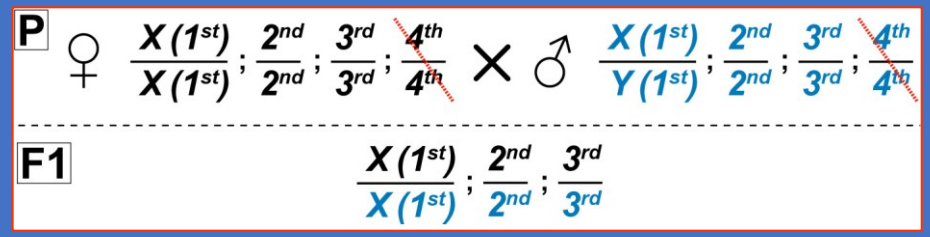
Figure 1 Simple and easy-to-grasp schematics illustrating common *Drosophila* marker mutations. All images were generated with the "Genotype Builder" Photoshop file (File S5). (A) The default set of flies (bristle, wing and eye markers set to "wildtype") displays wild-type body color (left column), ebony (middle column), and yellow (right column) and normal eye color (top row), white mutant eyes (middle row), and orange eyes (mini-white or $w^{apricot}$) (bottom row). (B) Example (top row only) with the settings "male" (fused abdominal stripe, sex combs, male anal plate), BRISTLES-Sb-Hu (Stubble$_{+/2}$, short blunt bristles; Humeral$_{+/2}$, multiplied humeral bristles), "EYE-wt" (normal shaped eyes) combined with OTHER-ry (*rosy*$^{-/-}$, brown eyes), "OTHER-Antp" (*Antennapedia*$^{+/-}$; antenna-to-leg transformation typical of the *Antp*^{73b} mutation), "WINGS-Cy-Ser" (*Curly*$^{+/-}$, curly wing; *Ser*$^{+/-}$, notched wing tips). (C) Example (top row only) with the settings "female" (nonfused abdominal stripes, little protrusions of anal plates), EYES-Dr (*Drop*$^{+/-}$, severely reduced eyes), "BRISTLES-sn" (*singed*$^{-/-}$; curled bristles) and WINGS-vg (*vestigial*$^{-/-}$; severely reduced wings).

“Learning to fly” poster

Drosophila mutant phenotypes



Rules to be used here:



- 'X' indicates the crossing step; female is shown on the left, male on the right
- sister chromosomes are separated by a horizontal line, different chromosomes are separated by a semicolon, the 4th chromosome will be neglected (crossed out)
- maternal chromosomes (inherited from mother) are shown above, paternal chromosomes (blue) below separating line
- the first chromosome represents the sex chromosome, which is either X or Y - females are *X/X*, males are *X/Y* (animals may be indicated as "X / Y or X" if both genders are being used or can be used)
- generations are indicated as P (parental), F1, 2, 3.. (1st, 2nd, 3rd.. filial generation)
- to keep it simple: dominant markers start with capital, recessive markers with lower case letters (but note that FlyBase nomenclature is more complex)

Some stocks from our lab

- *yellow, Adar^{5G1}, white* / FM7 *Bar*; ;
- *yellow, white;* (m*w*$^{+}$)*UAS-Adar* transgene construct / SM5 *Curly;*
- *white; Lobe /* SM5 *Curly; rosy, ebony /* TM3 *Stubble*
- Balancer chromosomes First chromosome multiple inversions FM7, Second multiple SM5, Third multiple TM3

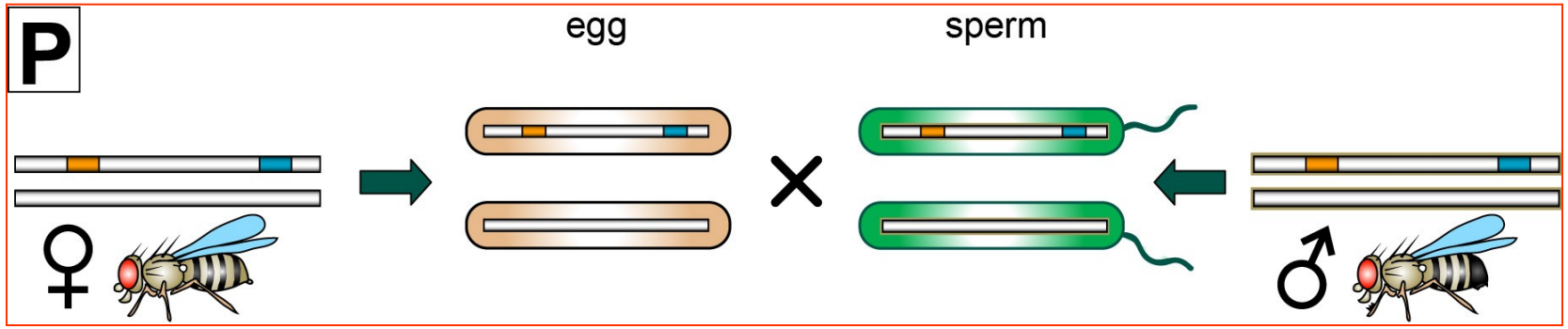
Balancer chromosomes

- What balancer chromosomes are.
- How we use them to keeps stocks with mutant genes or transgenes.

STEP2: Remind yourself of the basic rules of *Drosophila* genetics:

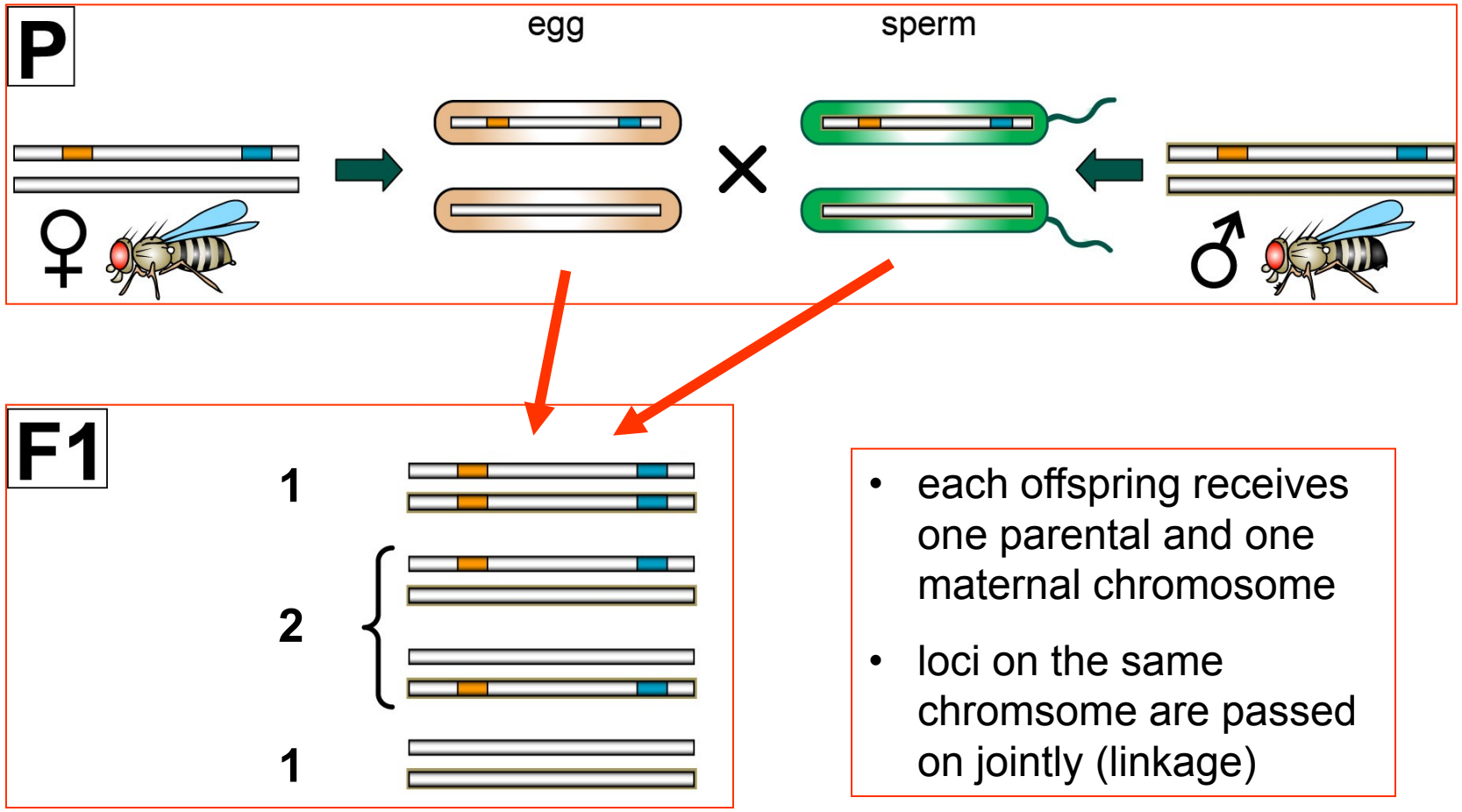
- law of segregation
- independent assortment of chromosomes
- linkage groups and recombination (recombination rule)
- balancer chromosomes and marker mutations

Law of segregation / linkage groups



Homologous chromosmes are separated during meiosis

Law of segregation / linkage groups



- each offspring receives one parental and one maternal chromosome
- loci on the same chromsome are passed on jointly (linkage)

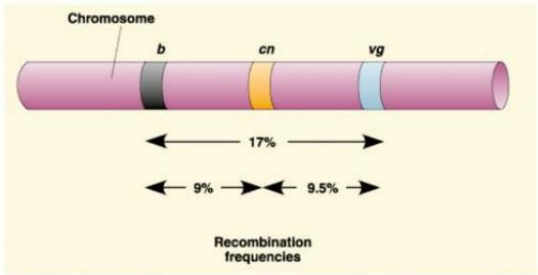
Genes on the same chromosome will recombine

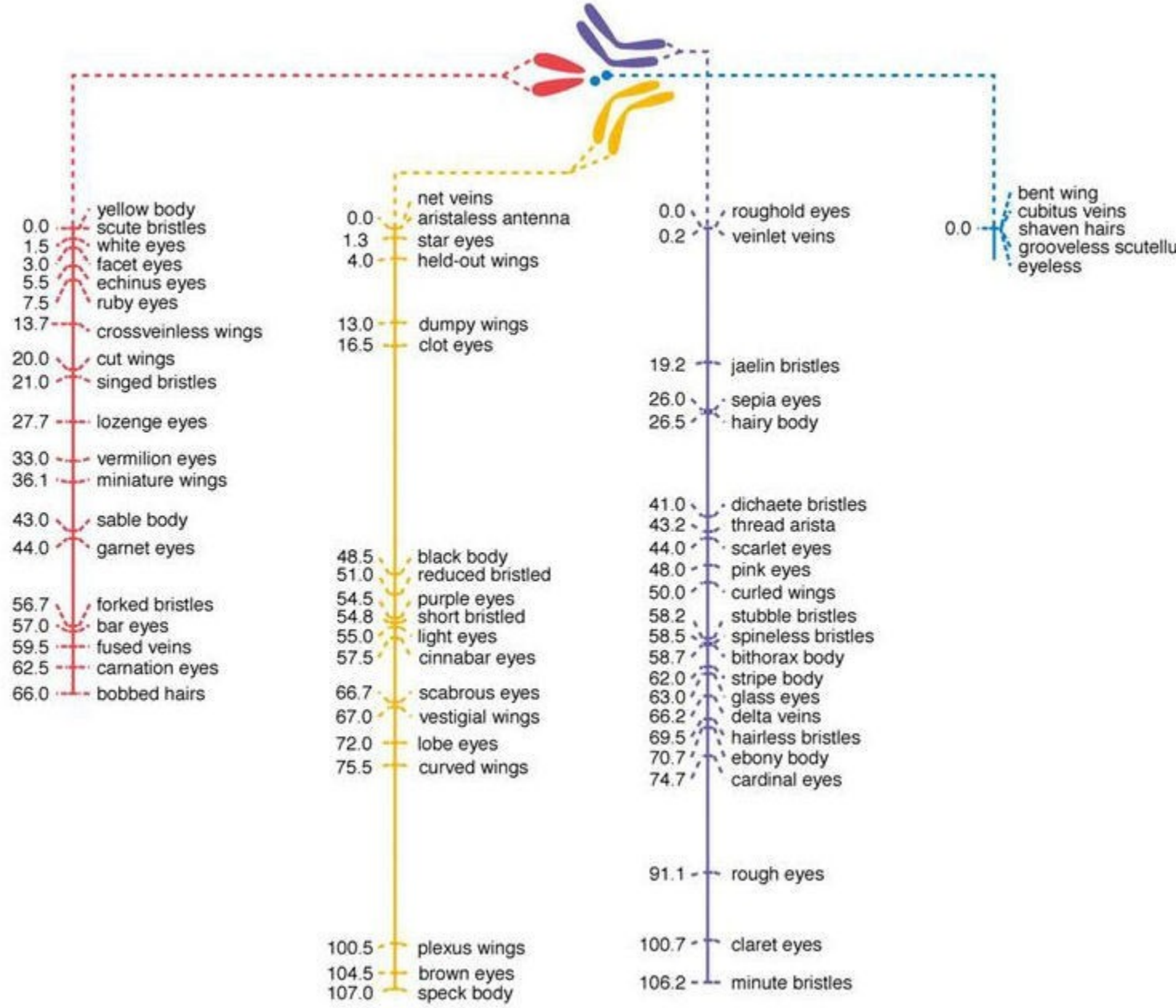
Sturtevant's linkage map of 3 genes in *Drosophila*

- 3 genes: body-color (b), wing-size (vg), and cinnebar (cn) –one of many genes affecting eye color
- Observed recombination frequencies:
  - cn and b = 9%
  - cn and vg = 9.5%
  - b and vg = 17%

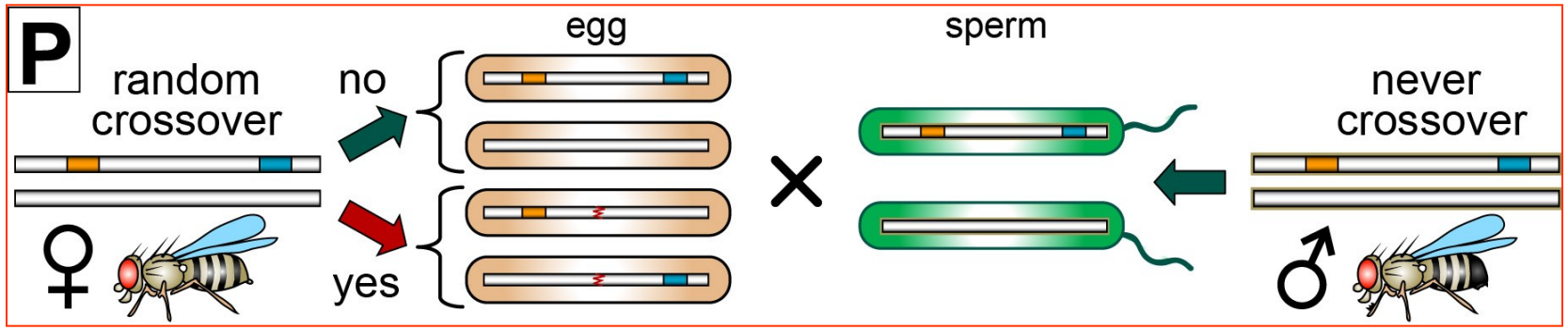
*Crossing over would occur most frequently between genes b and vg

- He decided to "map" these out on a chromosome
  - 1 map unit is = to 1% recombination frequency





Complication: recombination in females

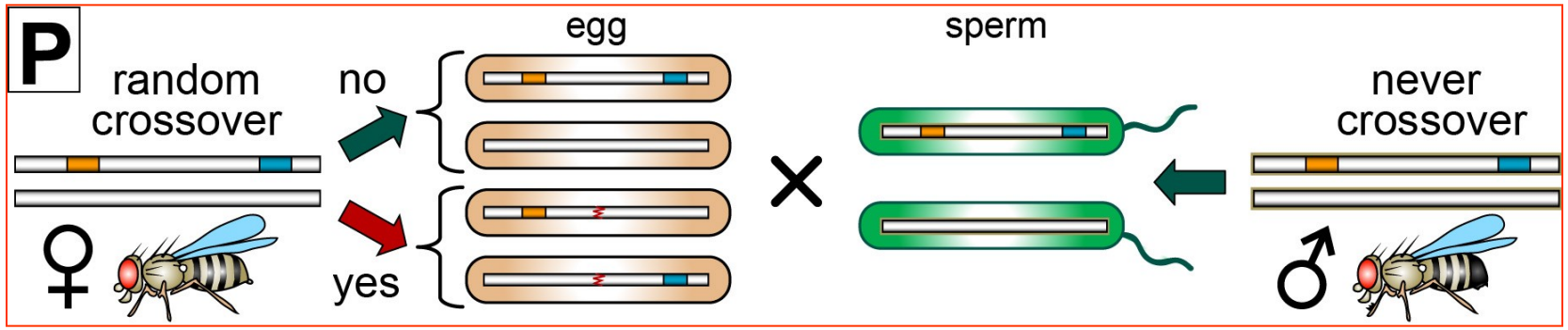


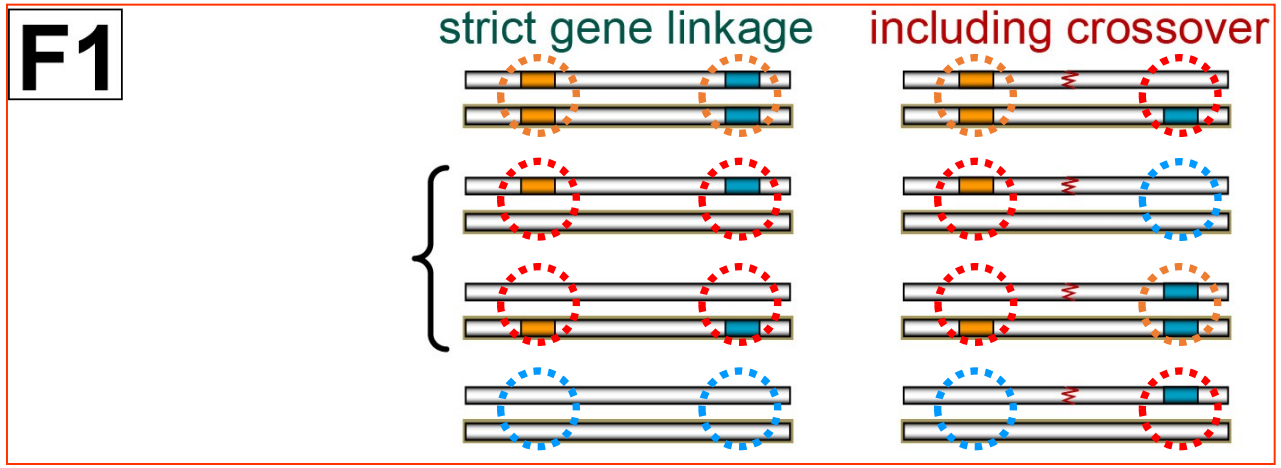
intra-chromosomal recombination takes place randomly during oogenesis

Recombination rule:

there is no recombination in males (nor of the 4th chromosome)

Complication: recombination in females

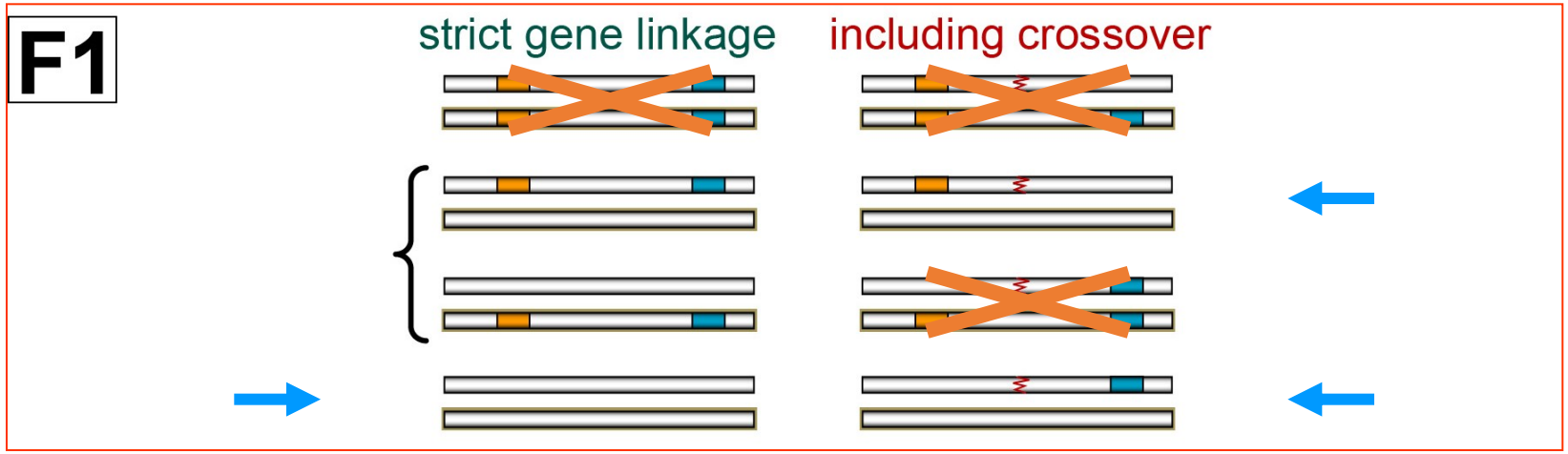




wildtype
heterozygous
homozygous
mutant

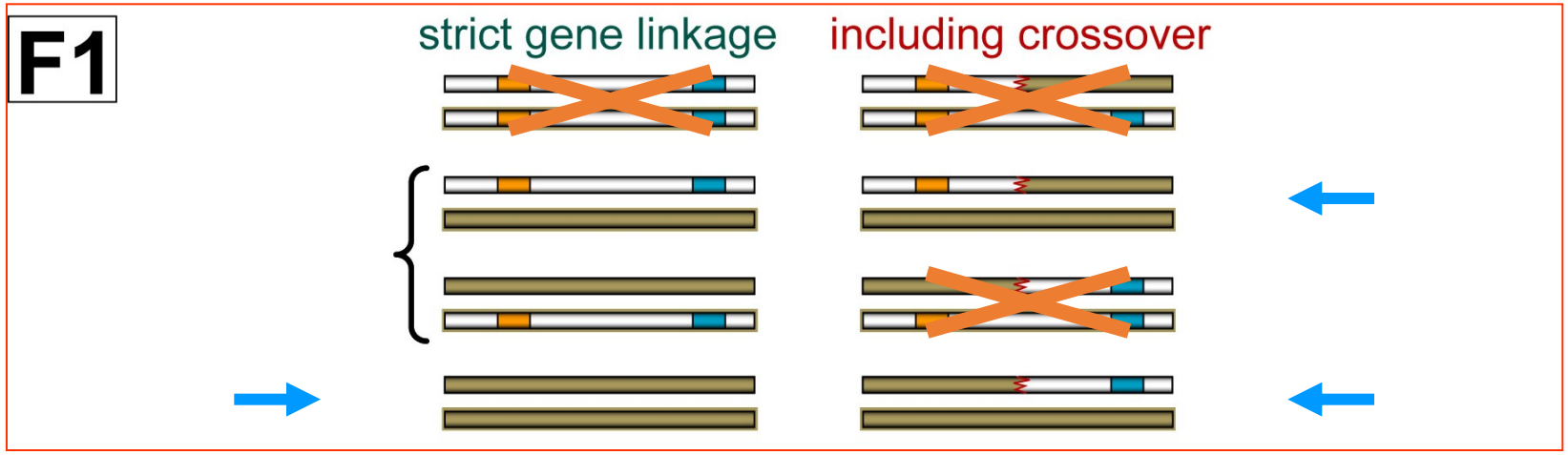
7 instead of 3 different genotypes

Balancers and stock keeping



- **lethal mutations are difficult to keep as a stock; they will gradually be lost** (i.e. be replaced by wt alleles in subsequent generations)

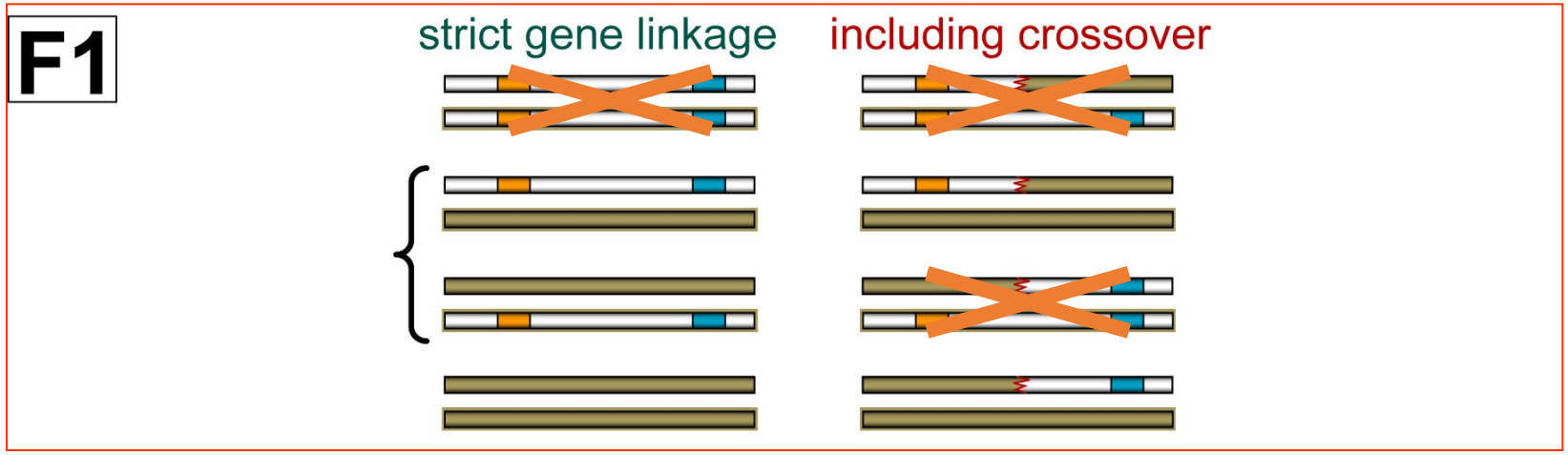
Balancers and stock keeping



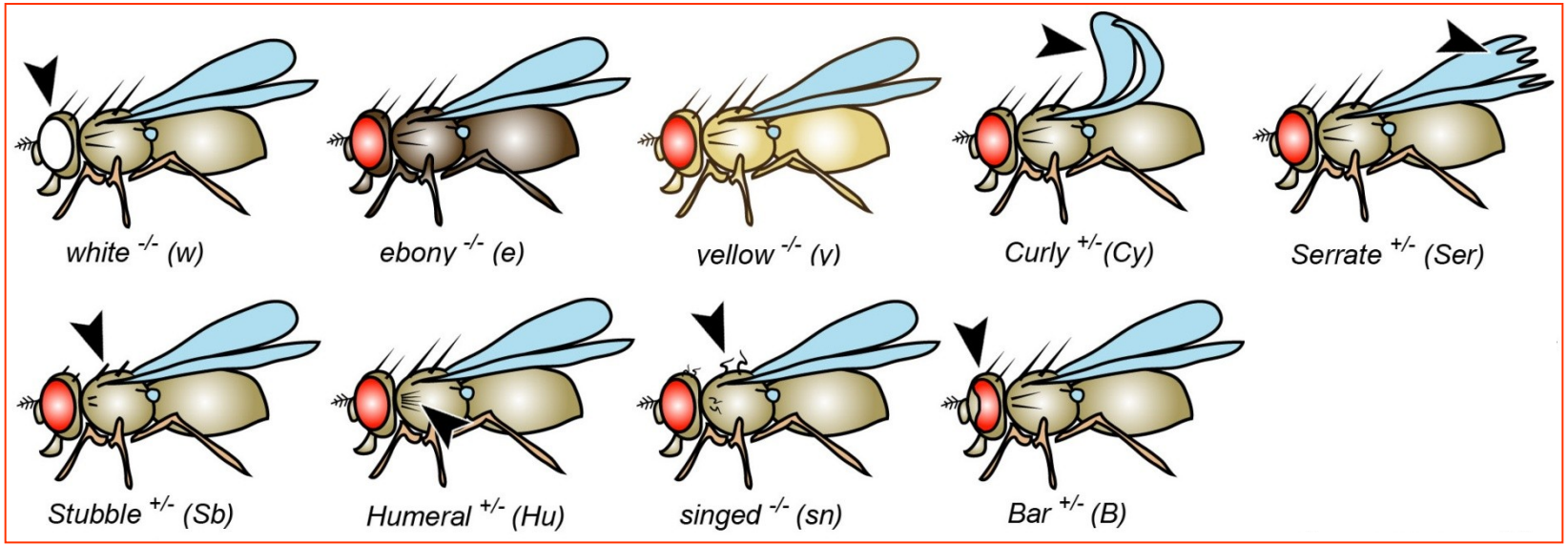
- **lethal mutations are difficult to keep as a stock; they will gradually be lost** (i.e. be replaced by wt alleles in subsequent generations)

- remedy in *Drosophila*: **balancer chromosomes**

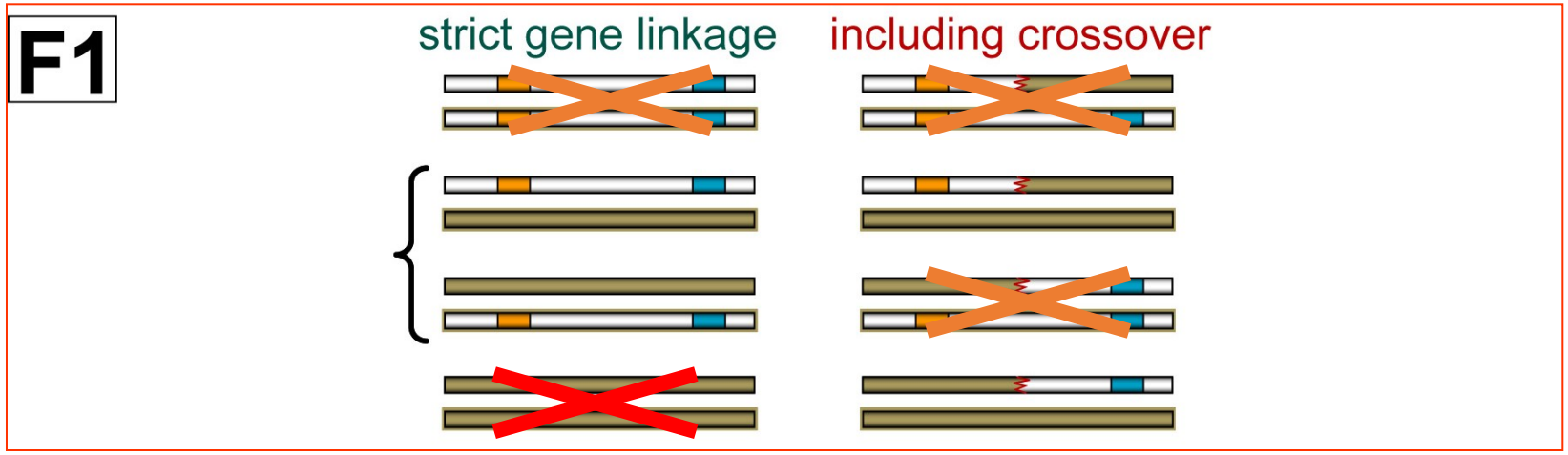
Balancers and stock keeping



- **balancers carry easily identifiable dominant and recessive markers**

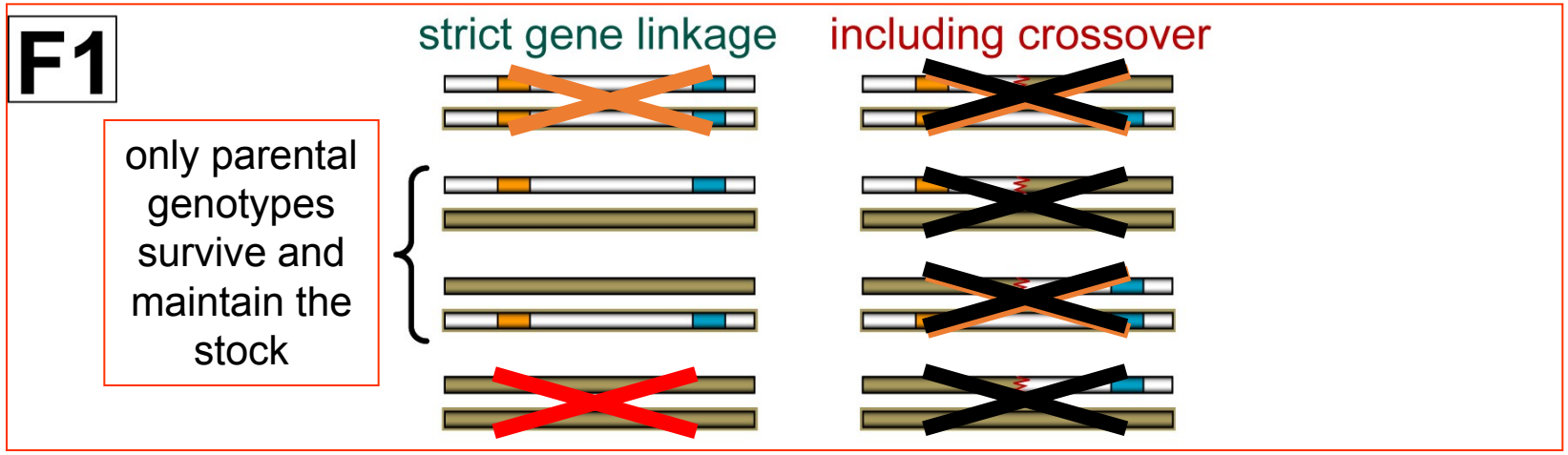


Balancers and stock keeping



- **balancers carry easily identifiable dominant and recessive markers**
- **balancers are homozygous lethal or sterile** (red cross)

Balancers and stock keeping



- **balancers carry easily identifiable dominant and recessive markers**
- **balancers are homozygous lethal or sterile** (red cross)
- **recombination of balancers is either suppressed or causes lethality** (black cross)

- Through using balancers, lethal mutations can be stably kept as stocks.
- In mating schemes, balancers can be used to prevent unwanted recombination.
- Balancers and their dominant markers can be used strategically to follow marker-less chromosomes through mating schemes.

- **Box 8. Examples of balancer chromosomes**

- Numerous balancer stocks are available from *Drosophila* stock centres (e.g. Bloomington / Balancers):

- **Typical standard balancers** (most marker mutations explained in Fig. 9):
- ***FM7a*** (*1st multiply-inverted 7a*) - X chromosome - typical markers: *y, wa, sn,* ***Bar1 (B1)***
- ***FM7c*** (*1st multiply-marked 7c*) - X chromosome - typical markers: *y*, *sc*, *w*, *oc*, *ptg*, ***B1***

- ***CyO*** (*Curly derivative of Oster*) - 2nd chromosome - typical markers: ***Cy*** **(*Curly*),** *dp* (*dumpy*; bumpy notum), *pr* (*purple*; eye colour), *cn2* (*cinnabar;* eye colour)
- ***SM6a*** (*2nd multiply-inverted 6a*) - 2nd chromosome - typical markers: *al*, ***Cy***, *dp*, *cn*, *sp*

- ***TM3*** (*3rd multiply-inverted 3)* - 3rd chromosome - typical markers: ***Sb****,* ***Ubx$^{bx\text{-}34e}$****,* (*bithorax*; larger halteres) *e,* ***Ser***
- ***TM6B*** (*3rd multiply-inverted 6B*) - 3rd chromosome – **Tb(Tubby)**

PLOS GENETICS

REVIEW

The joy of balancers

Danny E. Miller[1,2]*, **Kevin R. Cook**[3], **R. Scott Hawley**[4,5]*

1 Department of Medicine, Division of Medical Genetics, University of Washington, Seattle, Washington, United States of America, **2** Department of Pediatrics, Division of Genetic Medicine, University of Washington, Seattle, Washington and Seattle Children's Hospital, Seattle, Washington, United States of America, **3** Department of Biology, Indiana University, Bloomington, Indiana, United States of America, **4** Stowers Institute for Medical Research, Kansas City, Missouri, United States of America, **5** Department of Molecular and Integrative Physiology, University of Kansas Medical Center, Kansas City, Kansas, United States of America

* danny.miller@seattlechildrens.org (DEM); rsh@stowers.org (RSH)

Abstract

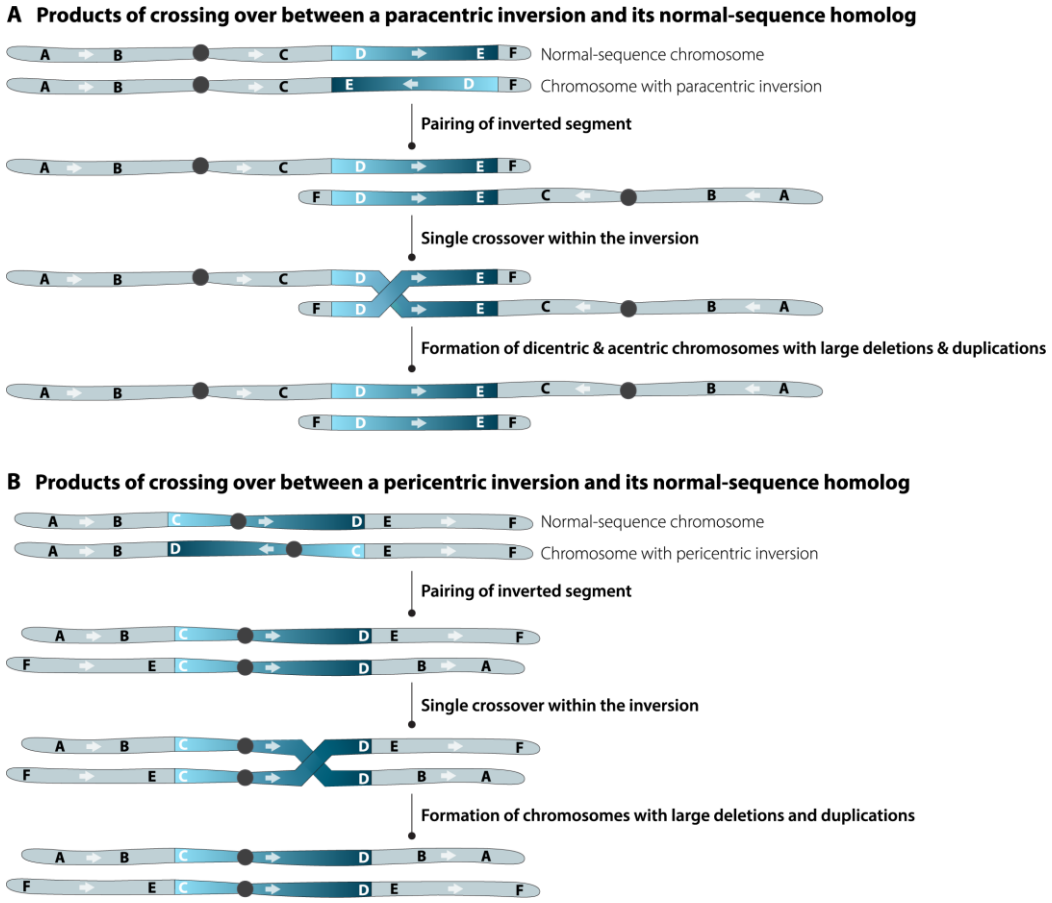
Balancer chromosomes are multiply inverted and rearranged chromosomes that are widely used in *Drosophila* genetics. First described nearly 100 years ago, balancers are used extensively in stock maintenance and complex crosses. Recently, the complete molecular structures of several commonly used balancers were determined by whole-genome sequencing. This revealed a surprising amount of variation among balancers derived from a common progenitor, identified genes directly affected by inversion breakpoints, and cataloged mutations shared by balancers. These studies emphasized that it is important to choose the optimal balancer, because different inversions suppress meiotic recombination in different chromosomal regions. In this review, we provide a brief history of balancers in *Drosophila*, discuss how they are used today, and provide examples of unexpected recombination events involving balancers that can lead to stock breakdown.

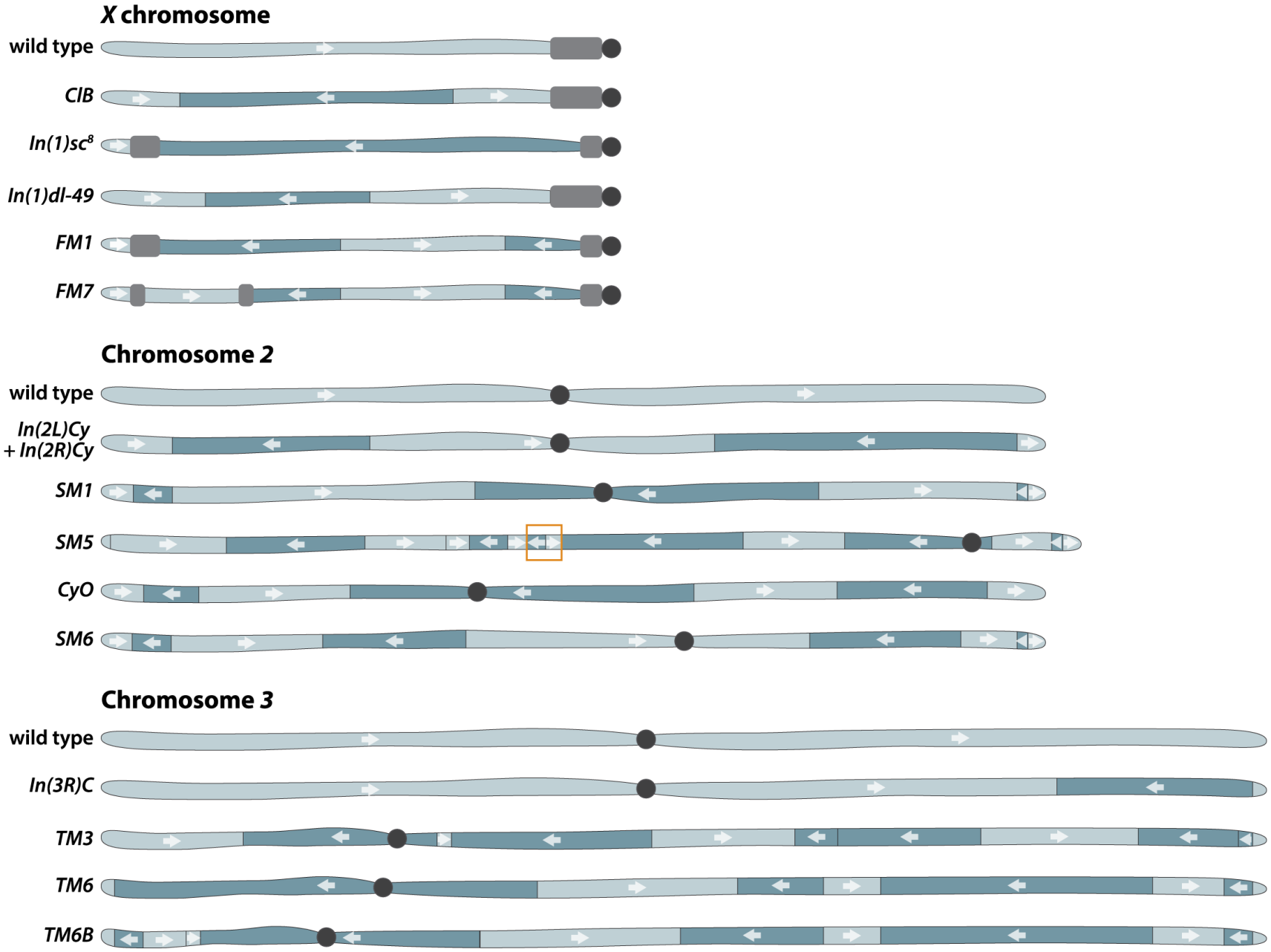
Citation: Miller DE, Cook KR, Hawley RS (2019) The joy of balancers. PLoS Genet 15(11): e1008421. https://doi.org/10.1371/journal.pgen.1008421

Editor: Gregory P. Copenhaver, The University of North Carolina at Chapel Hill, UNITED STATES

The tools and techniques of the *Drosophila* genetics trade have evolved dramatically over the last century, but one instrument has stood the test of time—the balancer chromosome. Balancers are now an omnipresent and indispensable tool in the fly lab, and their importance has been recognized in other organisms as well. The multiple inversions and rearrangements that

Recombination between two genes D and E was prevented by ‘balancing’ them over an inversion.




X chromosome
wild type
ClB
In(1)sc8
In(1)dl-49
FM1
FM7
Chromosome 2
wild type
In(2L)Cy
+ In(2R)Cy
SM1
SM5
CyO
SM6
Chromosome 3
wild type
In(3R)C
TM3
TM6
TM6B

- **Box 8. Examples of balancer chromosomes**

- Numerous balancer stocks are available from *Drosophila* stock centres (e.g. Bloomington / Balancers):

- **Typical standard balancers** (most marker mutations explained in Fig. 9):
- ***FM7a*** (*1st multiply-inverted 7a*) - X chromosome - typical markers: *y, wa, sn,* ***Bar1 (B1)***
- ***FM7c*** (*1st multiply-marked 7c*) - X chromosome - typical markers: *y*, *sc*, *w*, *oc*, *ptg*, ***B1***

- ***CyO*** (*Curly derivative of Oster*) - 2nd chromosome - typical markers: ***Cy*** **(*Curly*),** *dp* (*dumpy*; bumpy notum), *pr* (*purple*; eye colour), *cn2* (*cinnabar;* eye colour)
- ***SM6a*** (*2nd multiply-inverted 6a*) - 2nd chromosome - typical markers: *al*, ***Cy***, *dp*, *cn*, *sp*

- ***TM3*** (*3rd multiply-inverted 3)* - 3rd chromosome - typical markers: ***Sb****,* ***Ubx$^{bx\text{-}34e}$****,* (*bithorax*; larger halteres) *e,* ***Ser***
- ***TM6B*** (*3rd multiply-inverted 6B*) - 3rd chromosome – **Tb(Tubby)**

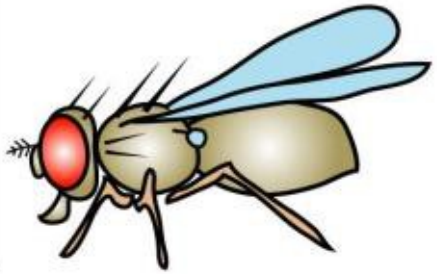
Primers on *Drosophila* genetics

- **Genetics** on the **Fly**: A Primer on the *Drosophila* Model System
- KG Hales, CA Korey, AM Larracuente, DM Roberts - **Genetics**, 2015 - academic.oup.com
- Read first half of this. Also history and glossary at the end

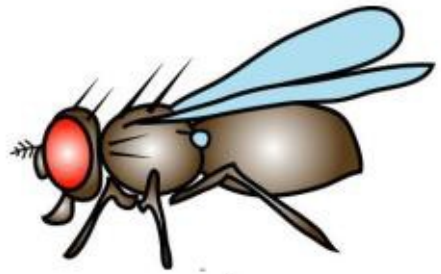
- The **joy** of **balancers**
- DE Miller, KR Cook, RS Hawley - PLoS genetics, 2019 - journals.plos.org
- Short. Read all of it. Learn which markers are most used for chromosome 1, 2 and 3 balancers

- How to Design a Genetic Mating Scheme: A Basic Training Package for *Drosophila* Genetics
- J **Roote**, A **Prokop** - G3: Genes| Genomes| Genetics, 2013 - academic.oup.com
- Look at supplementary files and read early parts. Gets too complicated later.

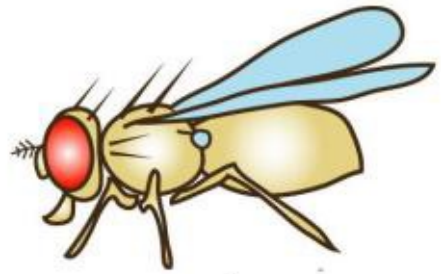
colour



wildtype

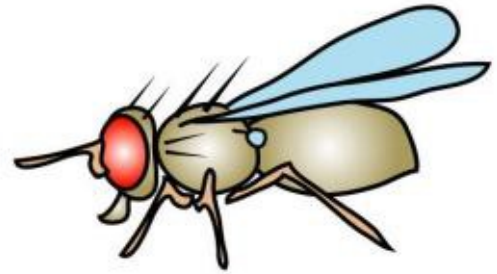


ebony $^{-/-}$ (e)



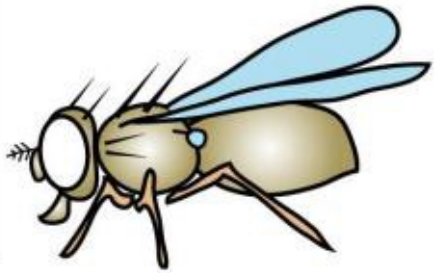
yellow $^{-/-}$ (y)

other

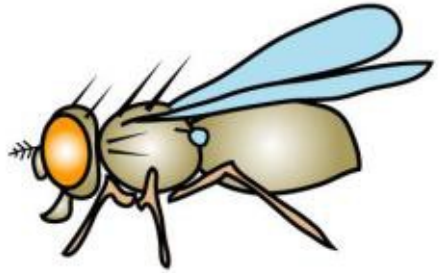


Antp $^{+/-}$ (Antp)

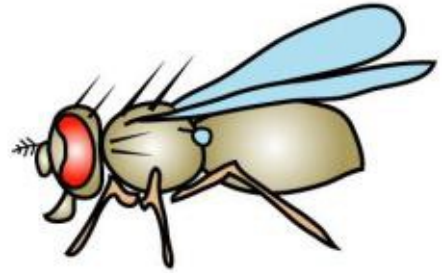
eyes



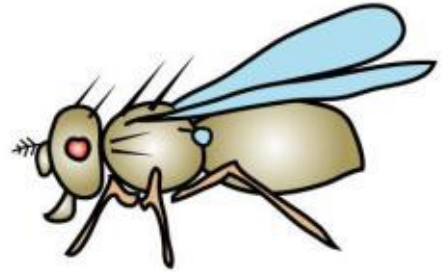
white $^{-/-}$ (w)



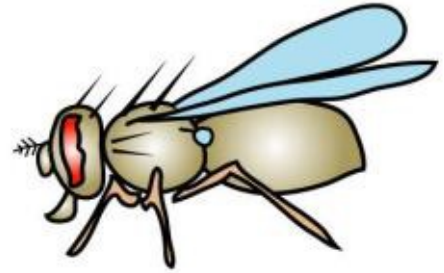
mini white (w^{+})



Bar $^{+/-}$ (B)

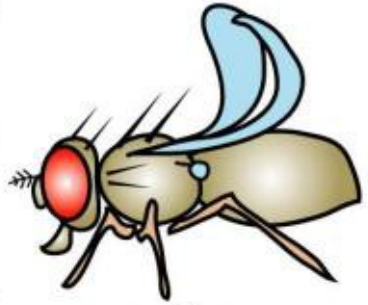


Drop $^{+/-}$ (Dr)

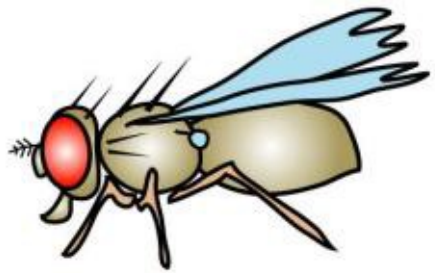


Irregular Facets $^{+/-}$ (If)

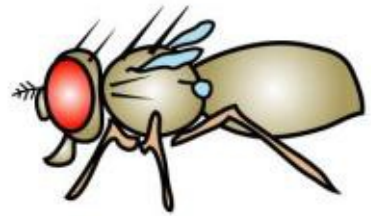
wings



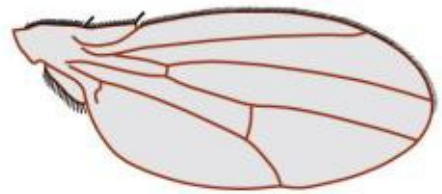
Curly $^{+/-}$(Cy)



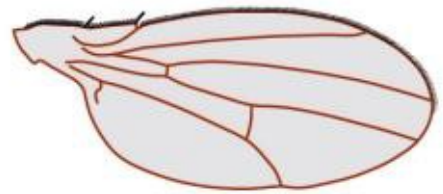
Serrate $^{+/-}$ (Ser)



vestigial $^{-/-}$ (vg)

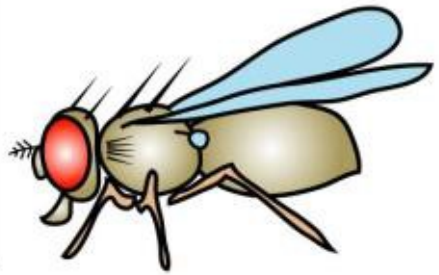


wildtype

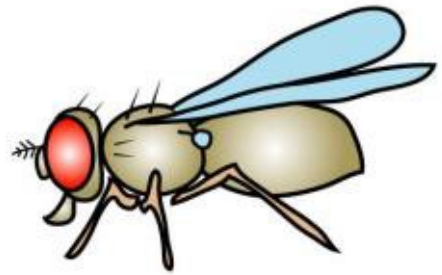


Dichaete (D)

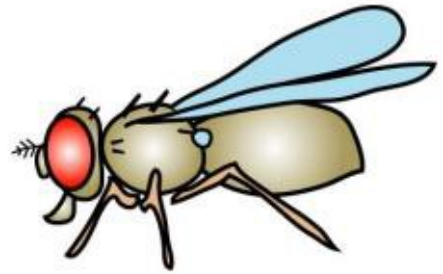
bristles



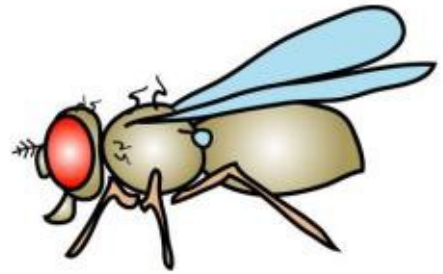
Humeral $^{+/-}$ (Hu)



Pin $^{+/-}$ (Pin)



Stubble $^{+/-}$ (Sb)

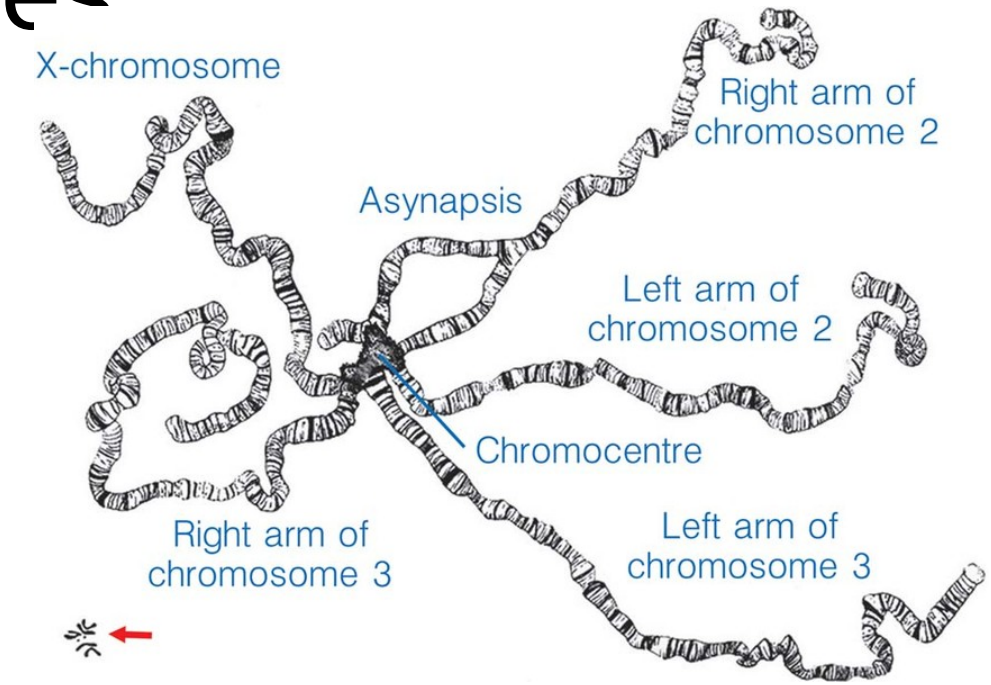


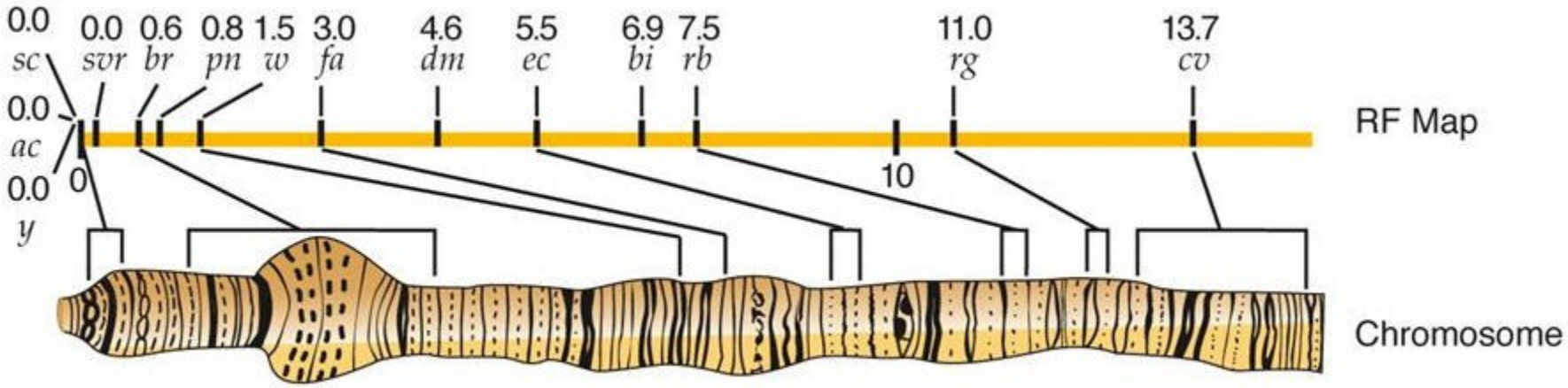
singed $^{-/-}$ (sn)

- **Figure 9.** Examples of typical marker mutations used during genetic crosses
- Mutations are grouped by body colour (top), eye markers (2nd row), wing markers (3rd row), bristle markers (bottom row), and "other" markers (top right). Explanations in alphabetic order:
- ○ *Antennapedia73b* (dominant; 3rd; antenna-to-leg transformation)
- ○ *Bar1* (dominant; 1st; kidney shaped eyes in heterozygosis, slit-shaped eyes in homo-/hemizygosis)
- ○ *Curly* (dominant; 2nd; curled-up wings; phenotype can be weak at lower temperatures, such as 18ºC)
- ○ *Dichaete* (dominant; 3rd; lack of alula, wings spread out)
- ○ *Drop* (dominant; 3rd; small drop-shaped eyes)
- ○ *ebony* (recessive; 3rd chromosome; dark body colour)
- ○ *Humeral* (dominant; 3rd; *Antennapedia* allele, increased numbers of humeral bristles)
- ○ *Irregular Facets* (dominant; 2nd; slit-shaped eyes)
- ○ *mini-white* (dominant in *white* mutant background, recessive in wildtype background; any chromosome; hypomorphic allele commonly used as marker on transposable elements)
- ○ *Pin* (dominant; 2nd; short pointed bristles)
- ○ *Serrate* (dominant; 3rd; serrated wing tips)
- ○ *singed* (recessive; 1st; curled bristles)
- ○ *Stubble* (dominant; 3rd; short, blunt bristles)
- ○ *vestigial* (recessive; 2nd; reduced wings)
- ○ *white* (recessive: 1st; white eye colour)
- ○ *yellow* (recessive; 1st; yellowish body colour)

- Photos of flies carrying marker mutations have been published elsewhere [29,31] 1.

Drosophila larval salivary gland polytene chromosomes





Polytene chromosome squash stained with Hoechst dye and anti-JIL1 histone kinase antibody

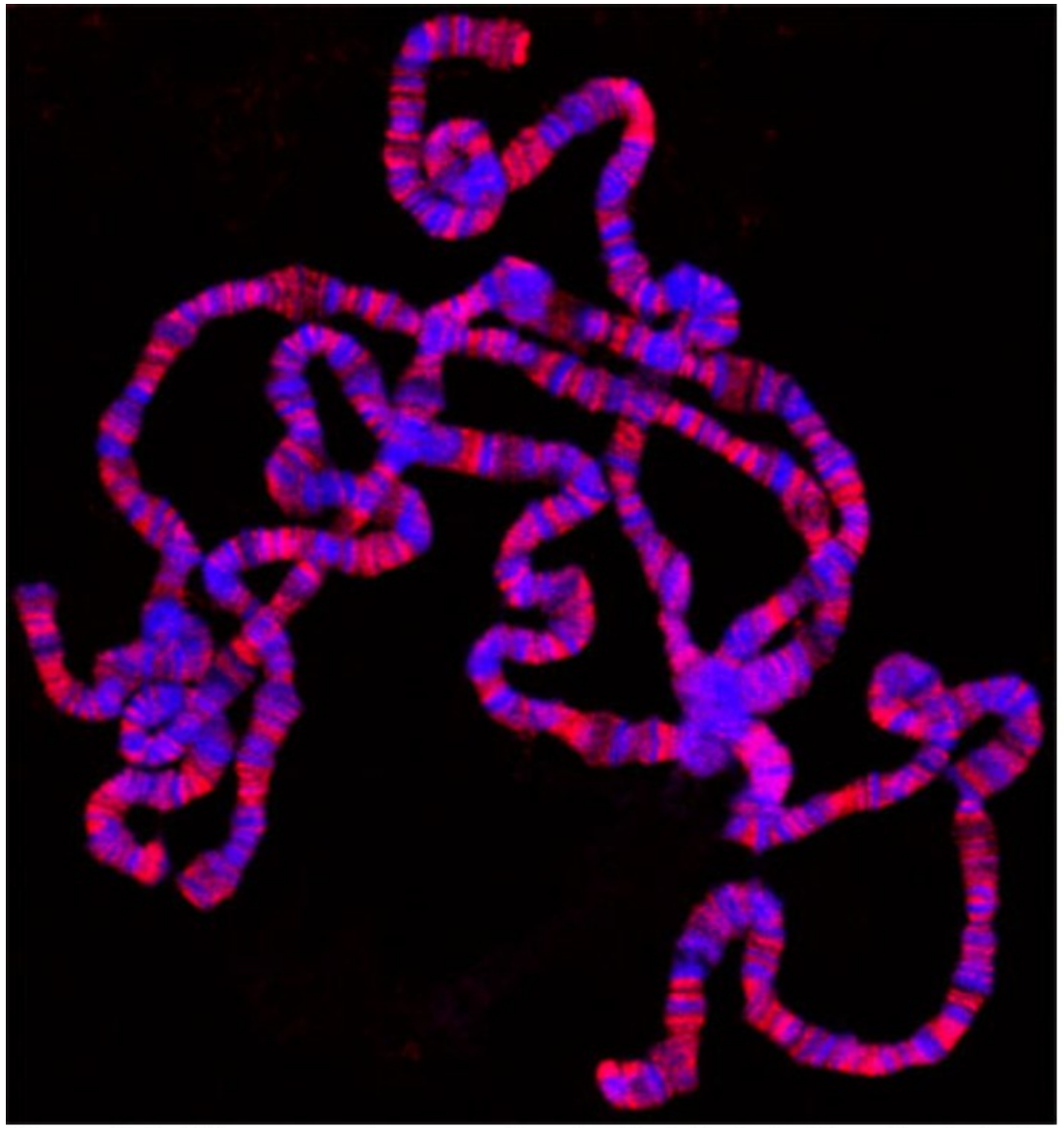
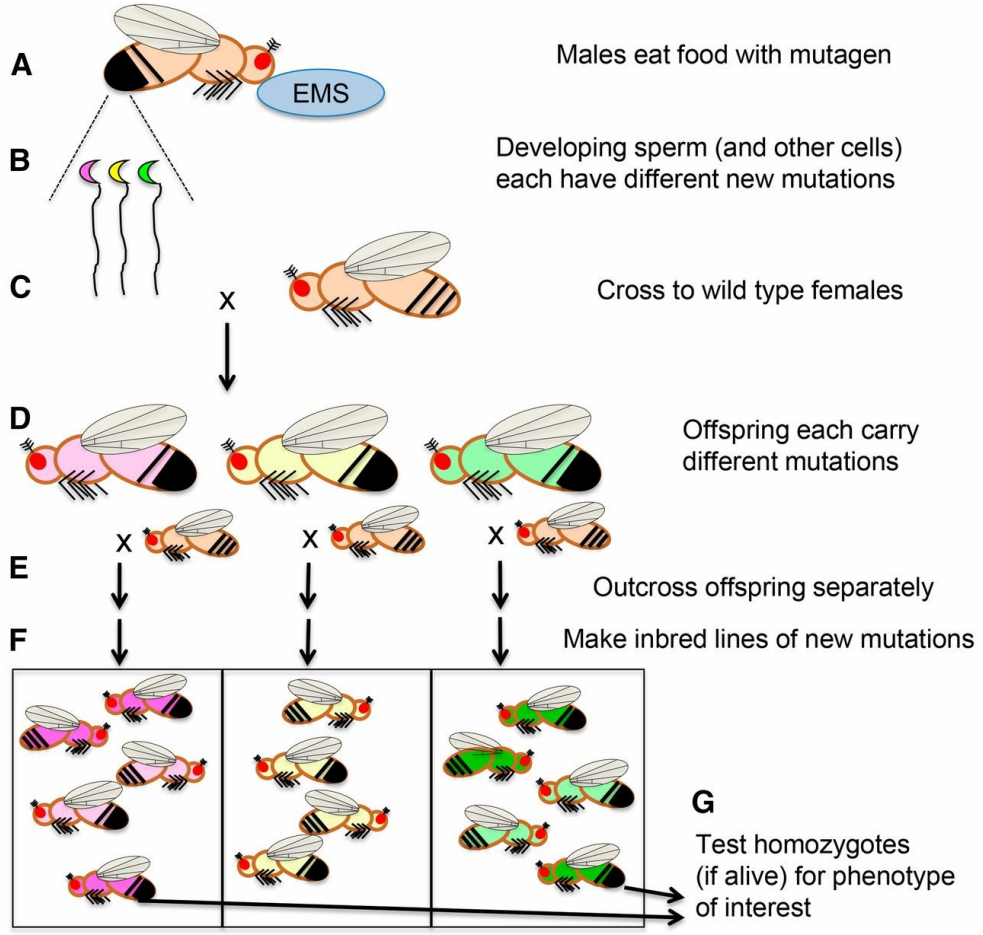


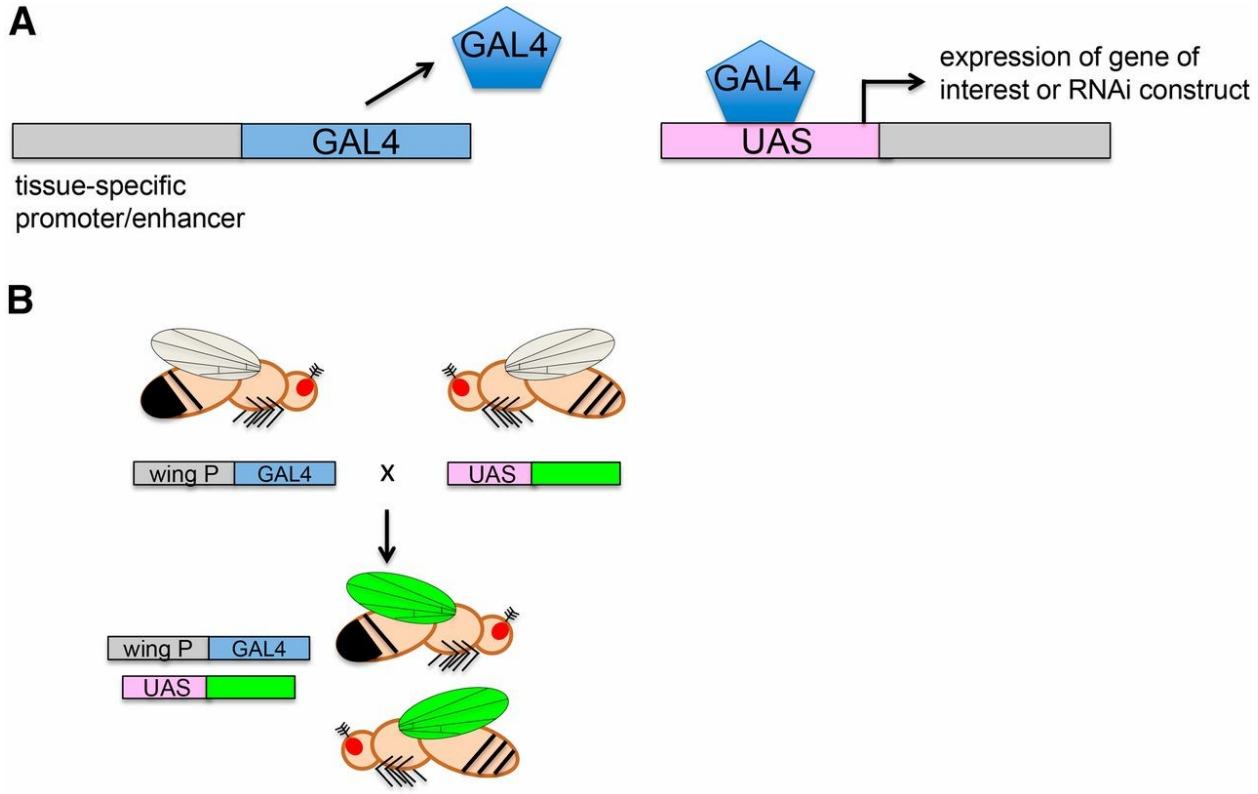
Figure 1. Polytene squash preparation double labeled with antibody to the JI

Figure 4 Generalized scheme for a forward genetic screen using chemical mutagenesis. (A) Male flies eat food laced ...



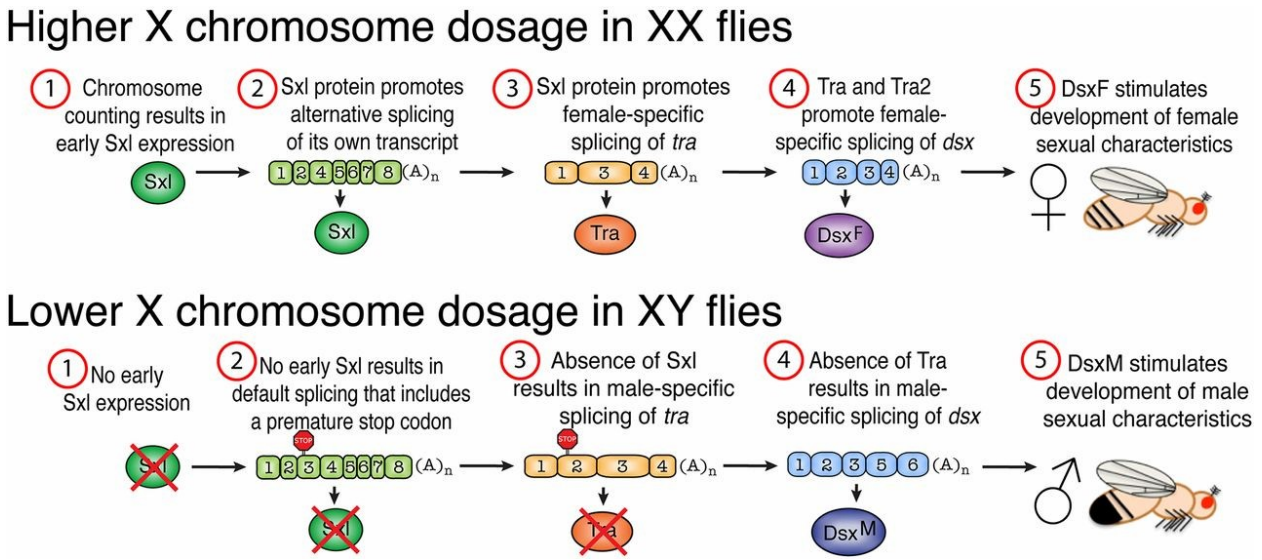
Genetics, Volume 201, Issue 3, 1 November 2015, Pages 815–842, https://doi.org/10.1534/genetics.115.183392

Figure 5 GAL4/UAS system for modular expression of transgenes in specific tissues. To express a transgene or RNAi ...



Genetics, Volume 201, Issue 3, 1 November 2015, Pages 815–842, https://doi.org/10.1534/genetics.115.183392

Figure 2 Sex determination. The number of X chromosomes in D. melanogaster is determined by an X chromosome counting ...



Genetics, Volume 201, Issue 3, 1 November 2015, Pages 815–842, https://doi.org/10.1534/genetics.115.183392