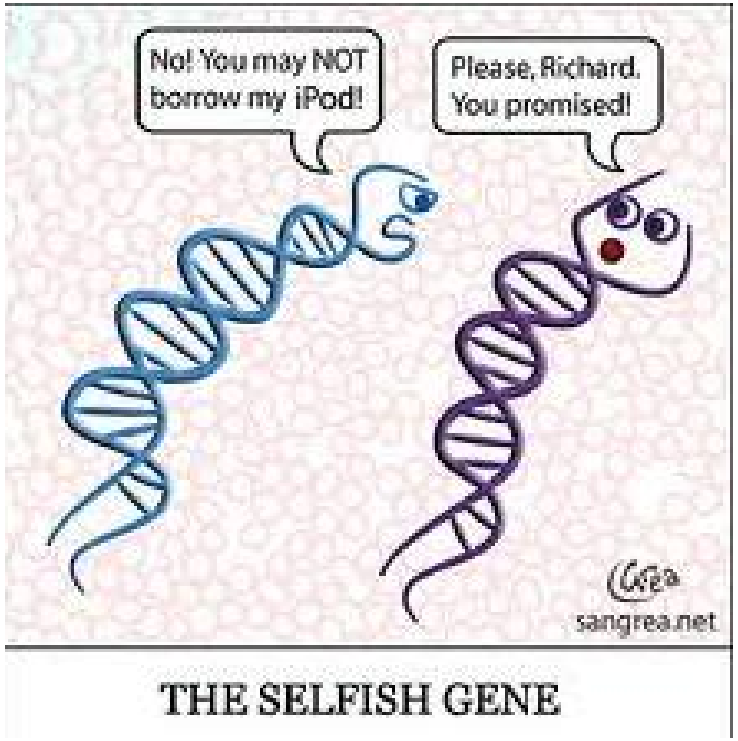
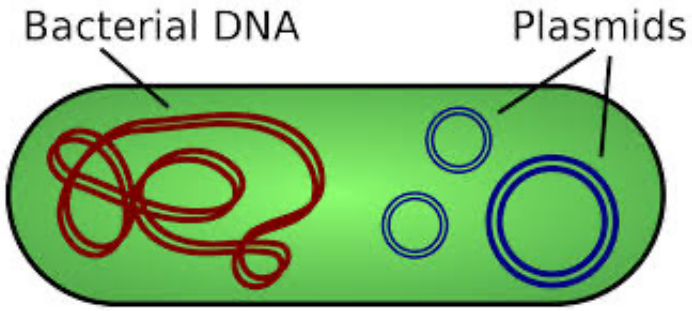
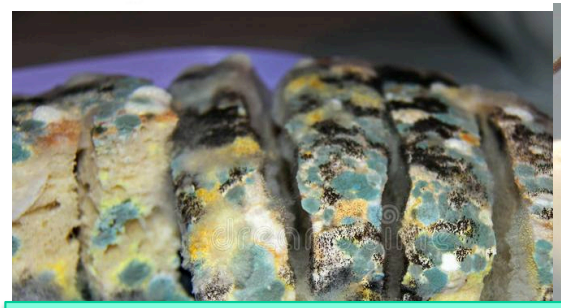
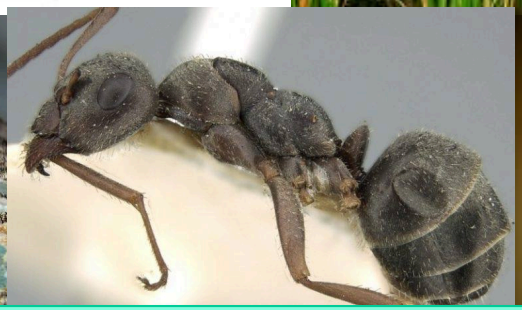
# Transposable elements: Selfish genes





Toxin-Antidote Elements Across the Tree of Life. Burga A, Ben-David E, Kruglyak L
Annu Rev Genet. 2020 Nov 23;54:387-415. doi: 10.1146/annurev-genet-112618-043659.

ANNUAL REVIEWS

*Annual Review of Genetics*

# Toxin-Antidote Elements Across the Tree of Life

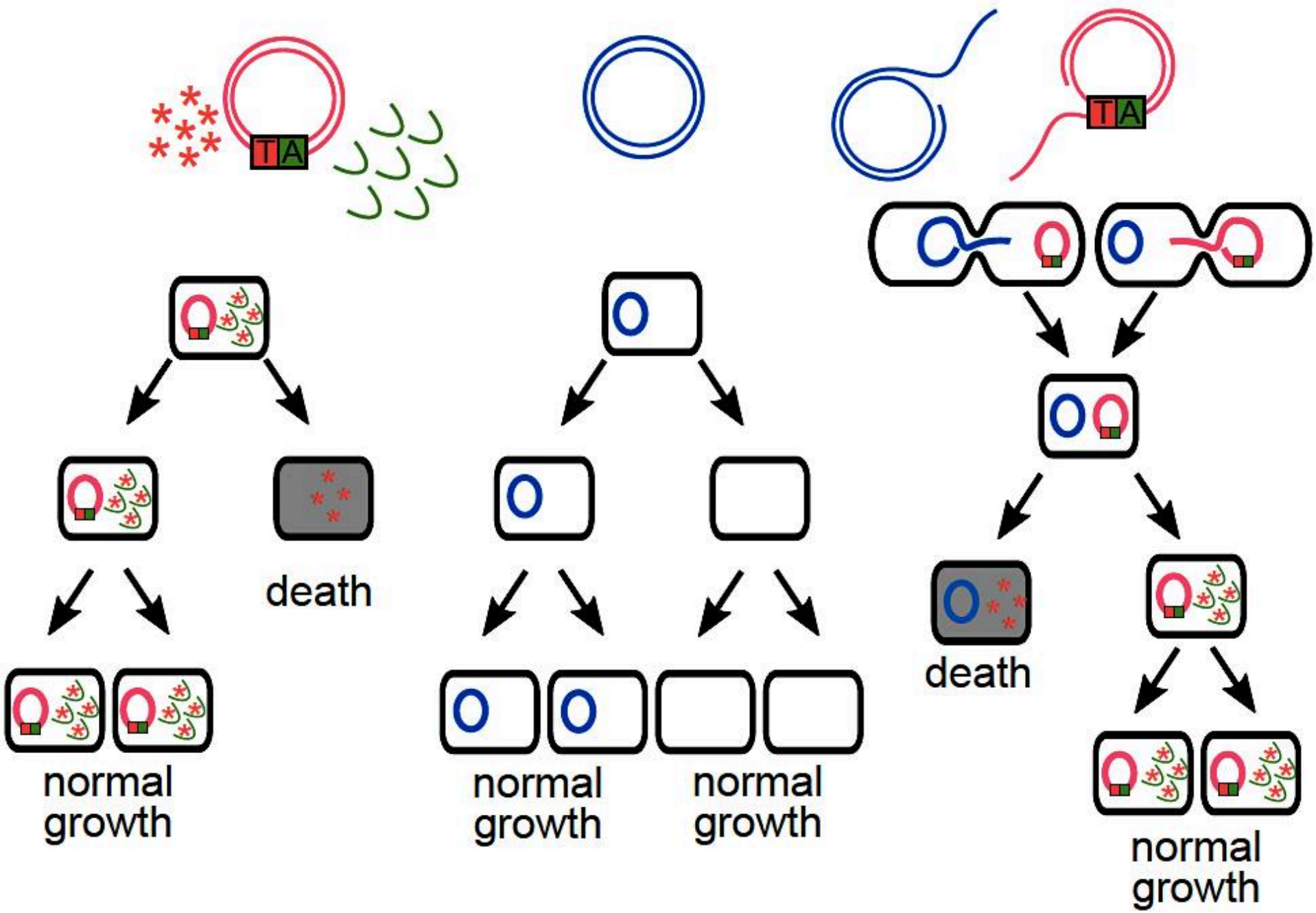
Alejandro Burga,[1,*] Eyal Ben-David,[2,3,*] and Leonid Kruglyak[2]

[1]Institute of Molecular Biotechnology of the Austrian Academy of Sciences (IMBA), Vienna BioCenter (VBC), 1030 Vienna, Austria; email: alejandro.burga@imba.oeaw.ac.at

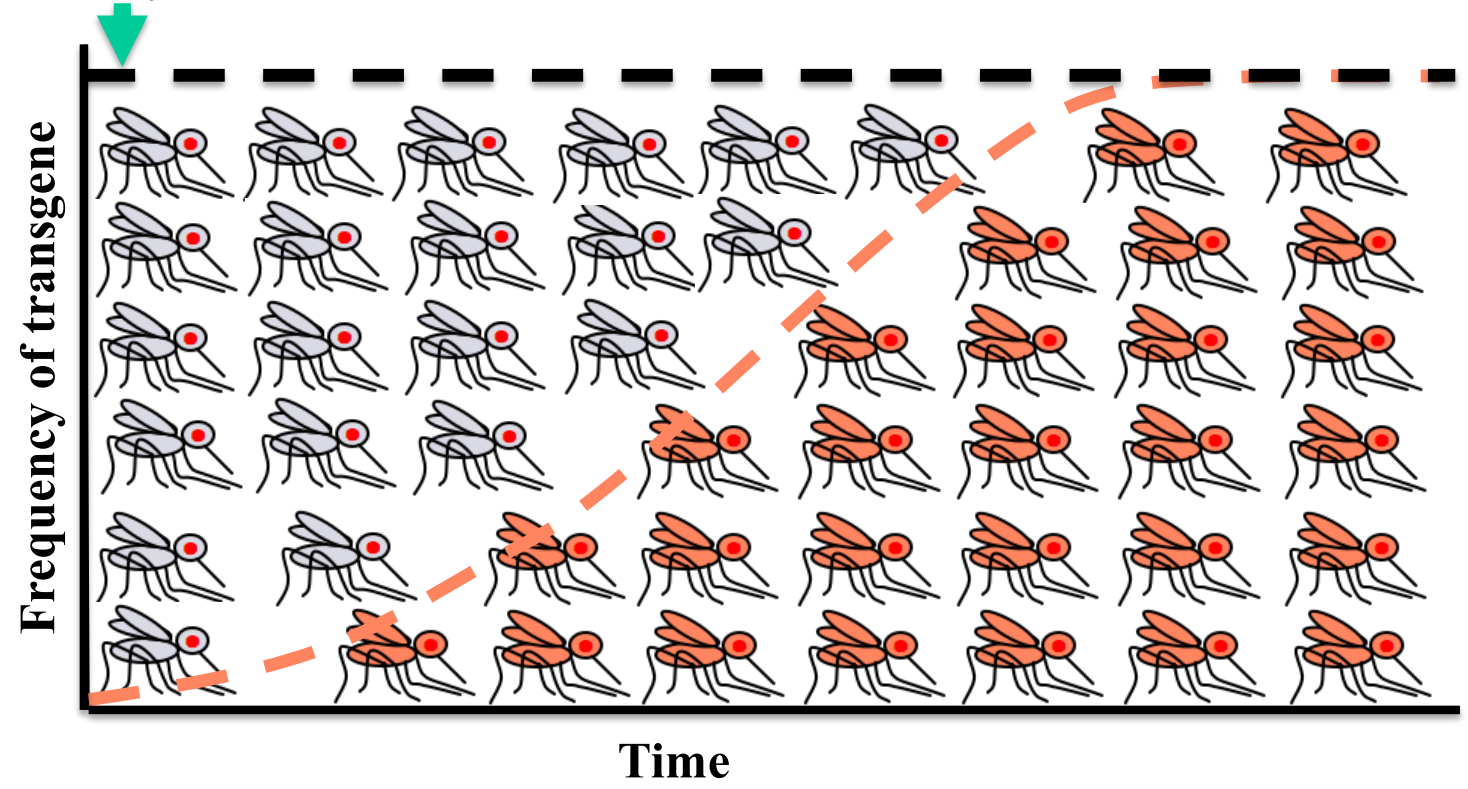
[2]Department of Human Genetics, Department of Biological Chemistry, and Howard Hughes Medical Institute, University of California, Los Angeles, California 90095, USA; email: lkruglyak@mednet.ucla.edu

[3]Department of Biochemistry and Molecular Biology, Institute for Medical Research Israel-Canada, The Hebrew University School of Medicine, Jerusalem 91120, Israel; email: eyal.bendavid@mail.huji.ac.il

**TA cassettes “encourage” their own transmission and kick plasmids of the same incompatibiity group that lack them out of the population**

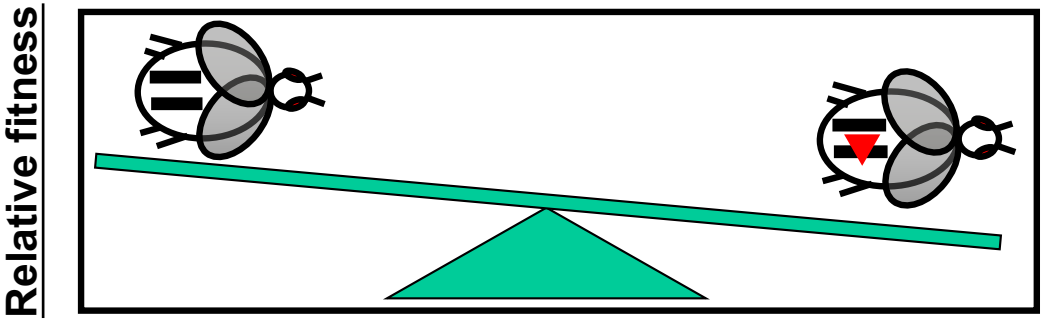


**Modify the wild population so that its members no longer cause harm (disease)**




**The challenge: How do we cause a trait to rapidly spread throughout a population?**

# Problem: traits of interest usually result In some fitness cost to carriers



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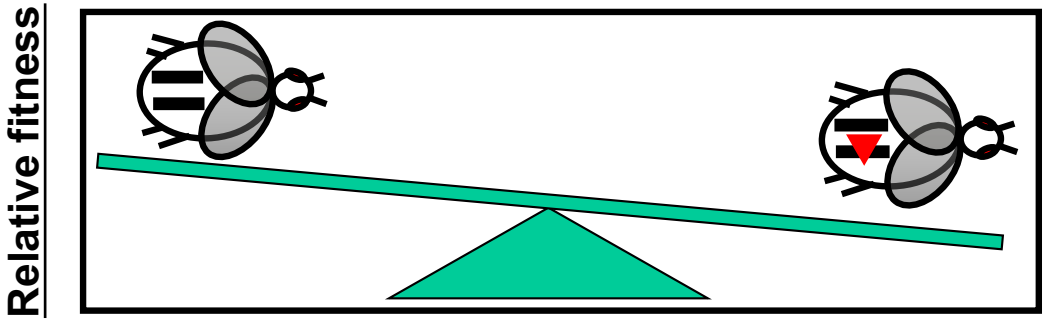
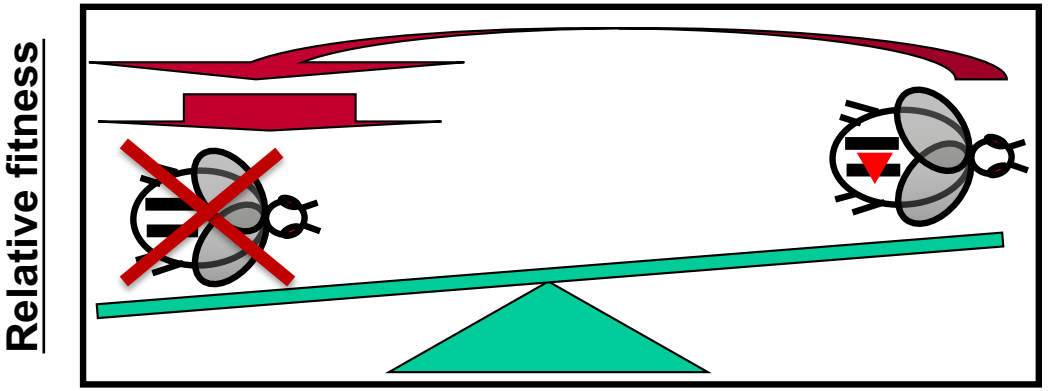
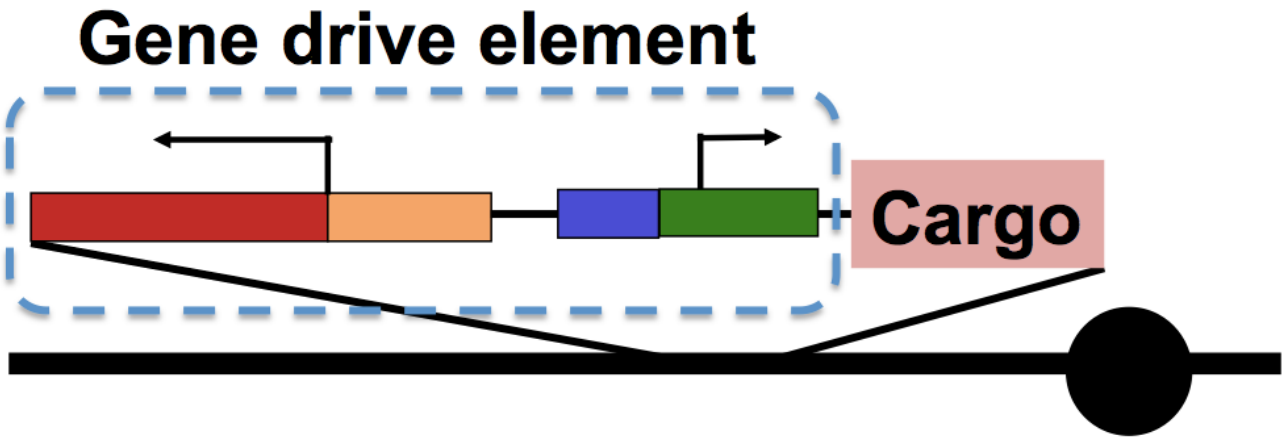



**Solution: Increase the fitness cost associated with NOT carrying the gene of interest**

**A form of Gene drive**



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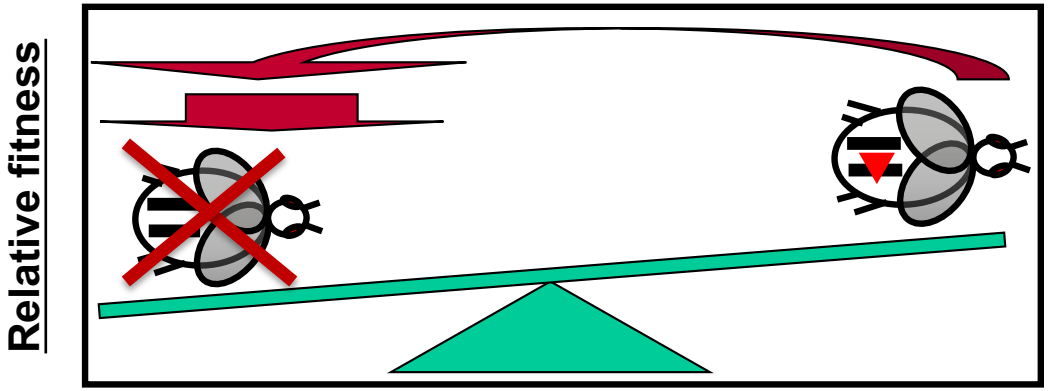
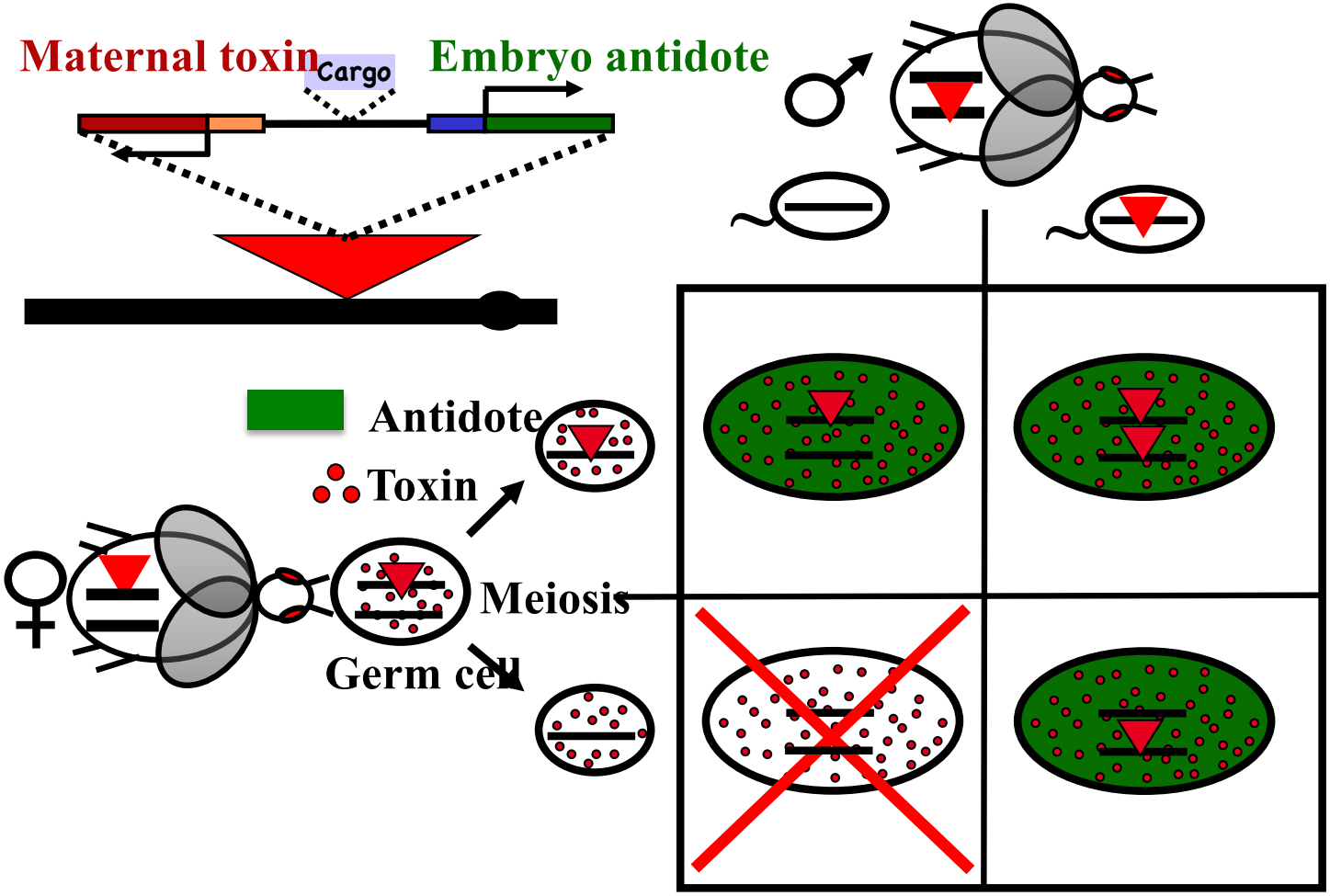
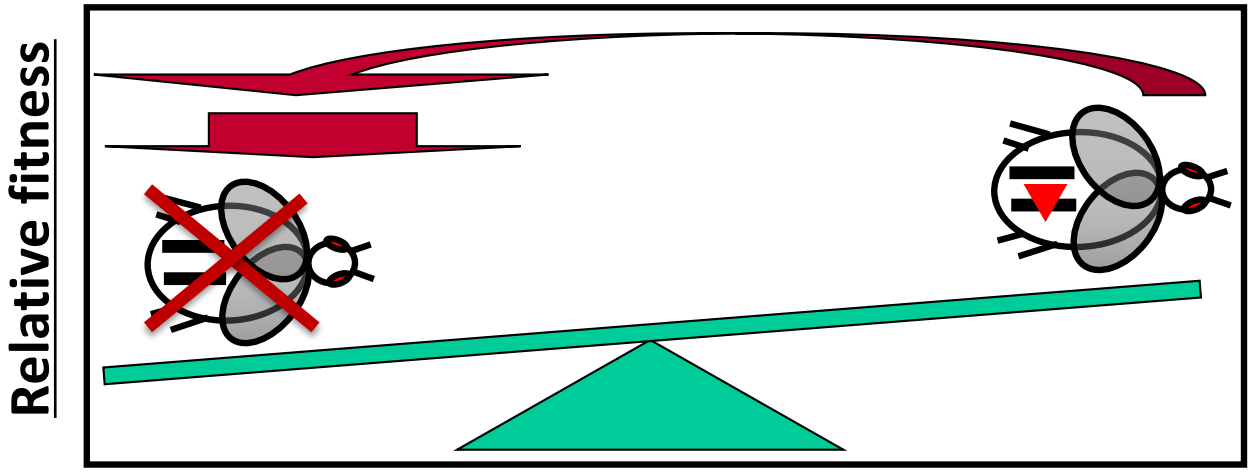


## *Medea* in insects: A maternal toxin deposited into all eggs. Only those inheriting the antidote survive

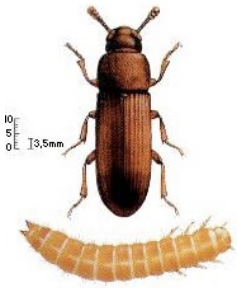





# *Medea*

# Cleave and Rescue (*ClvR*)

# *Medea* (▼), a novel selfish genetic element



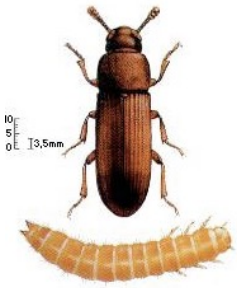

**Inheritance is Mendelian**



Beeman et al., (1992) Science 256, 89

# *Medea* (▼), a novel selfish genetic element

**When *Medea* (▼) is present in females, only progeny that inherit *Medea* survive**



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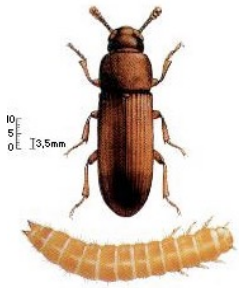
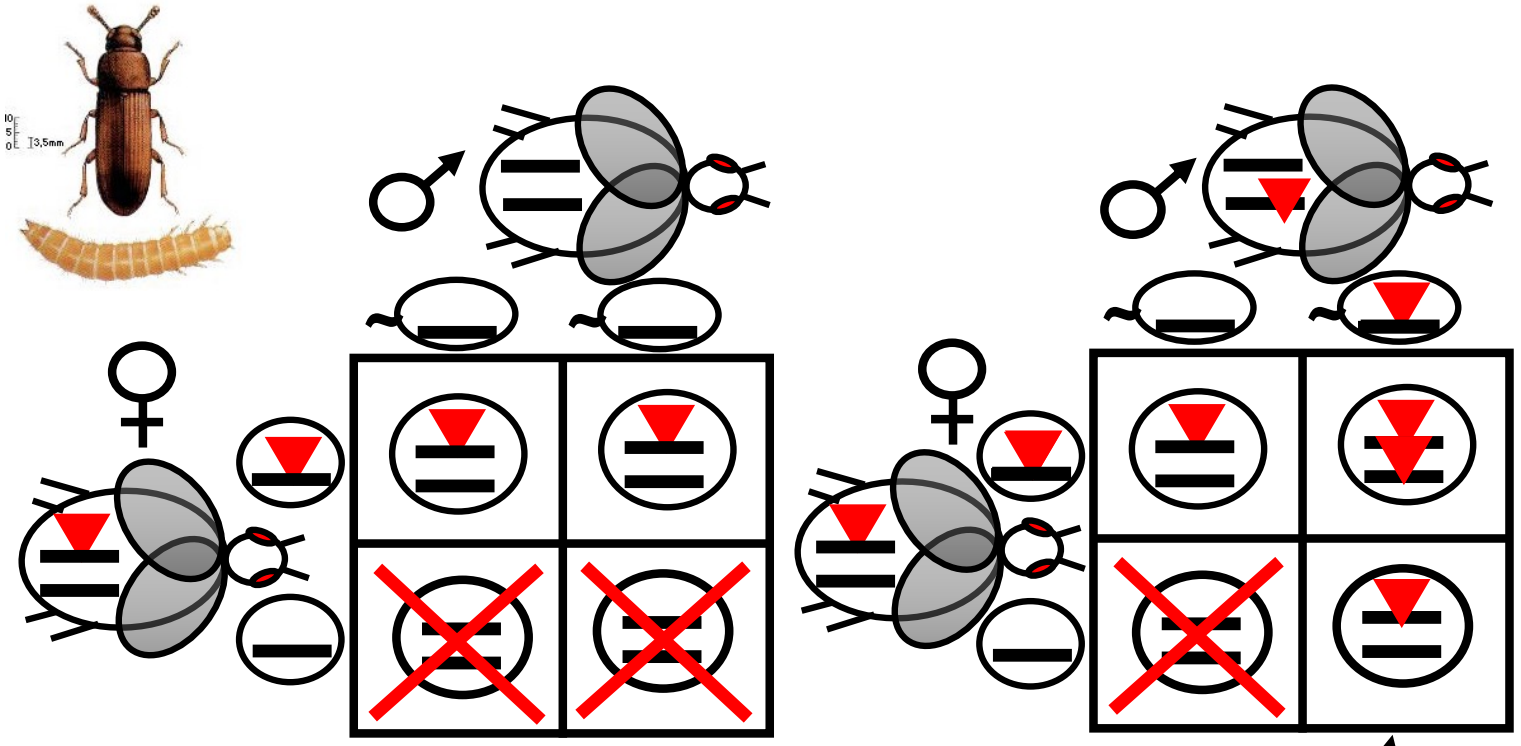





Beeman et al., (1992) Science 256, 89

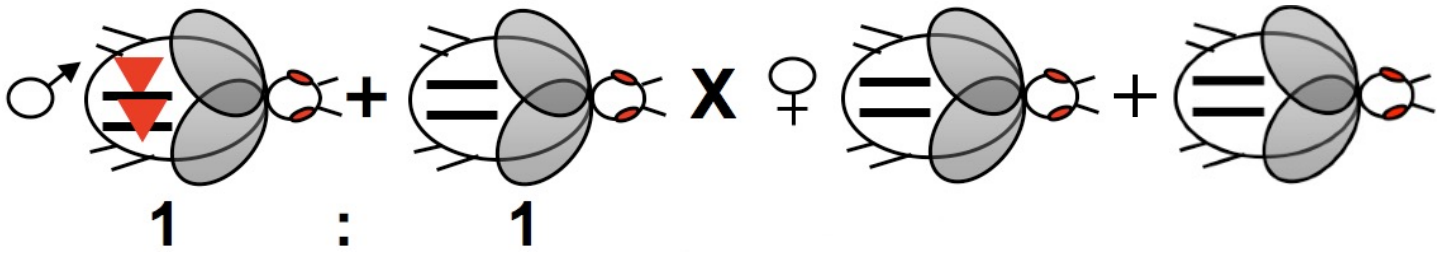
Paternal rescue

***Medea* gains a transmission advantage, not by increasing fitness of those that carry it, but by causing the death of those that lack it.**




Beeman et al., (1992) Science 256, 89

# *Medea* spreads, eliminating non-*Medea* individuals




Fraction *Medea* individuals in population

1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0

0
5
10
15
20

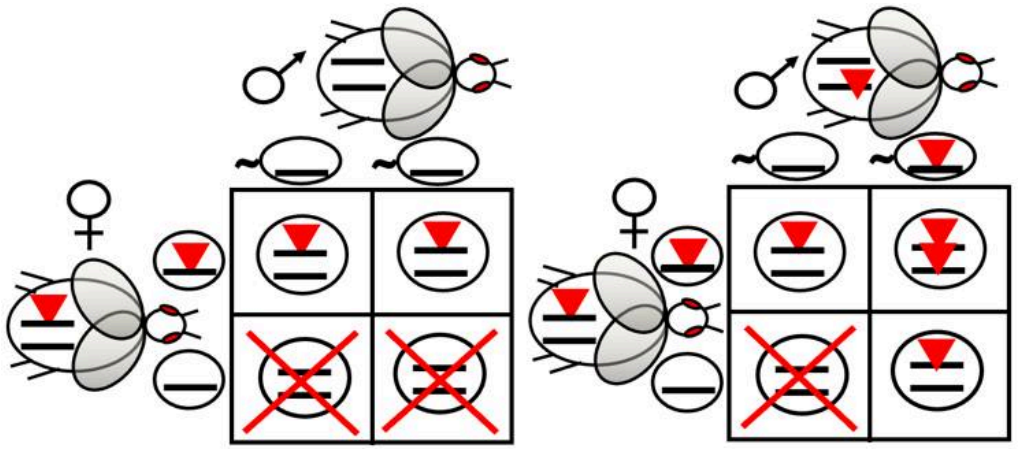
Generation

Fitness cost = 0

Fitness cost = 0.05

Fitness cost = 0.10

Fitness cost = 0.15



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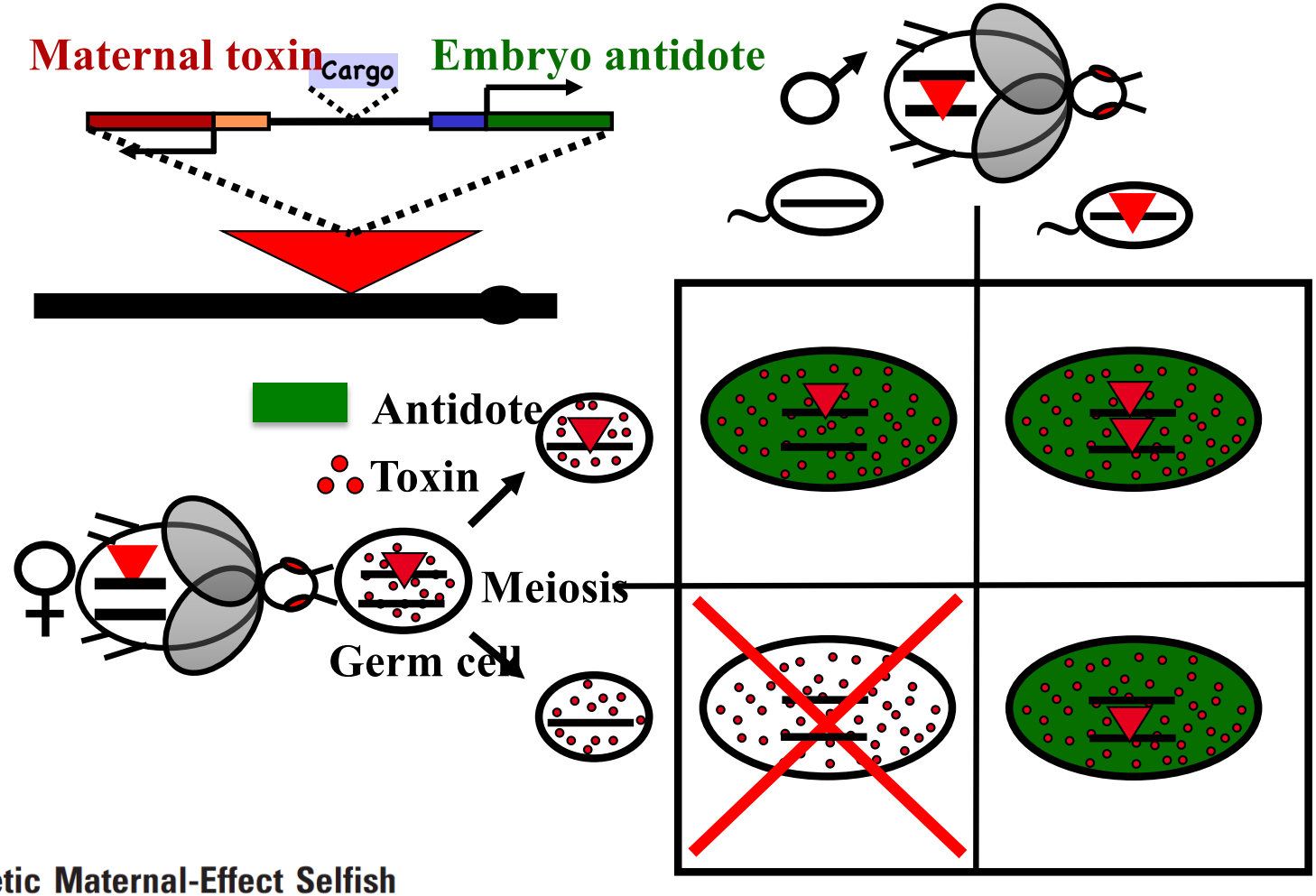
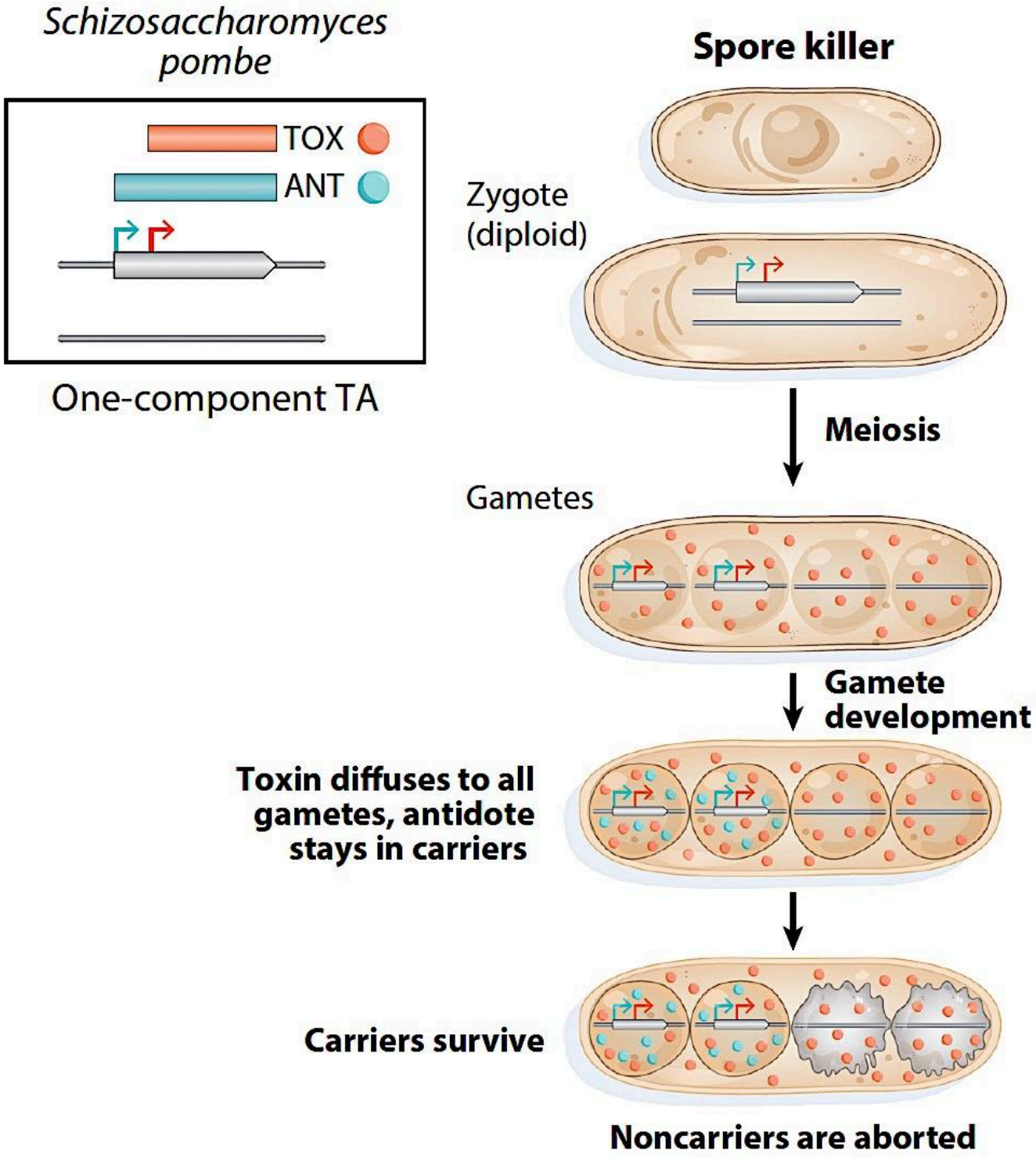



**A Synthetic Maternal-Effect Selfish Genetic Element Drives Population Replacement in *Drosophila***

Chun-Hong Chen,[1] Haixia Huang,[1] Catherine M. Ward,[1] Jessica T. Su,[1] Lorian V. Schaeffer,[1] Ming Guo,[2] Bruce A. Hay[1]*

Science
AAAS


Schizosaccharomyces pombe
TOX
ANT
One-component TA
Spore killer
Zygote (diploid)
Meiosis
Gametes
Gamete development
Toxin diffuses to all gametes, antidote stays in carriers
Carriers survive
Noncarriers are aborted

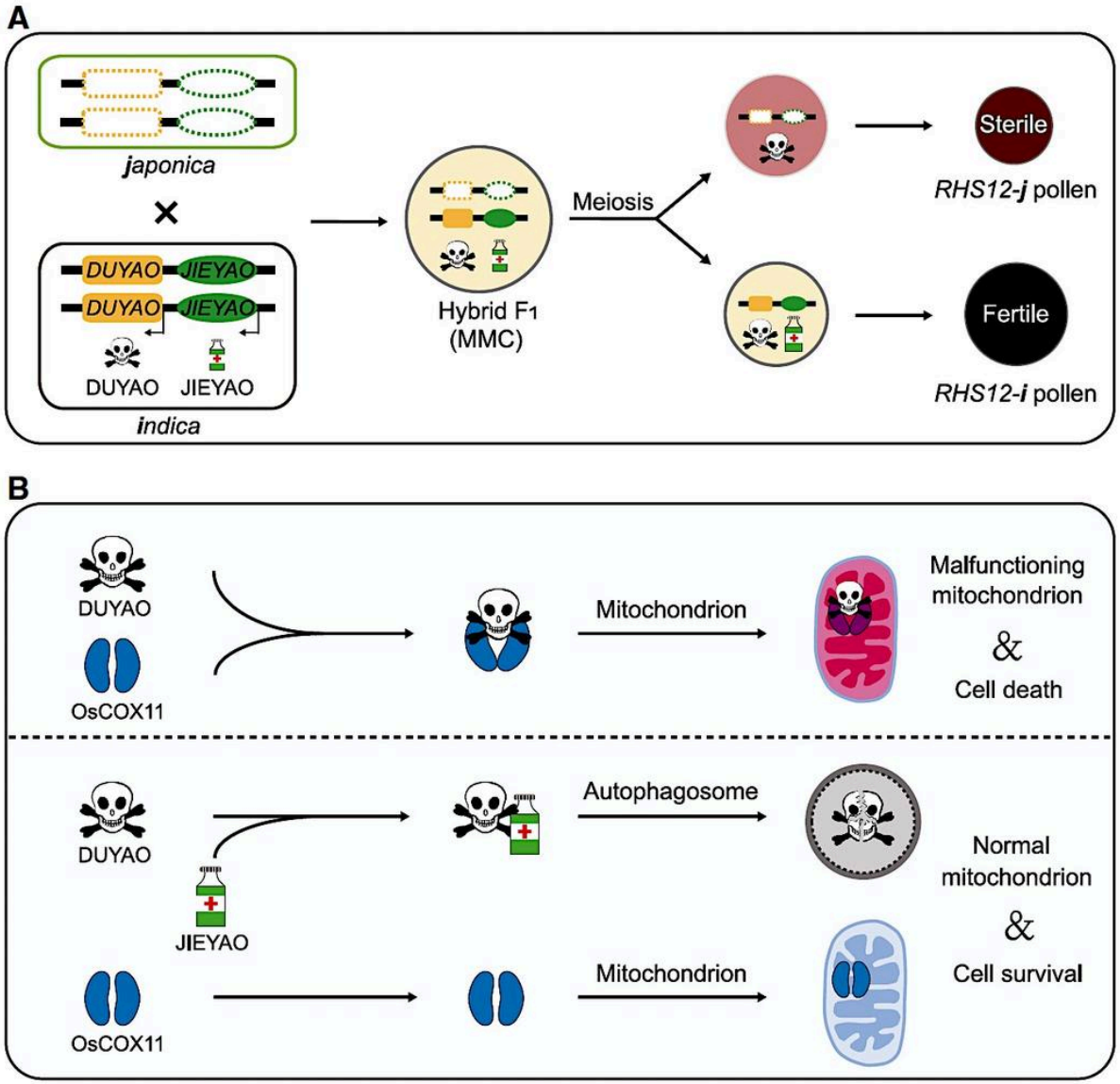
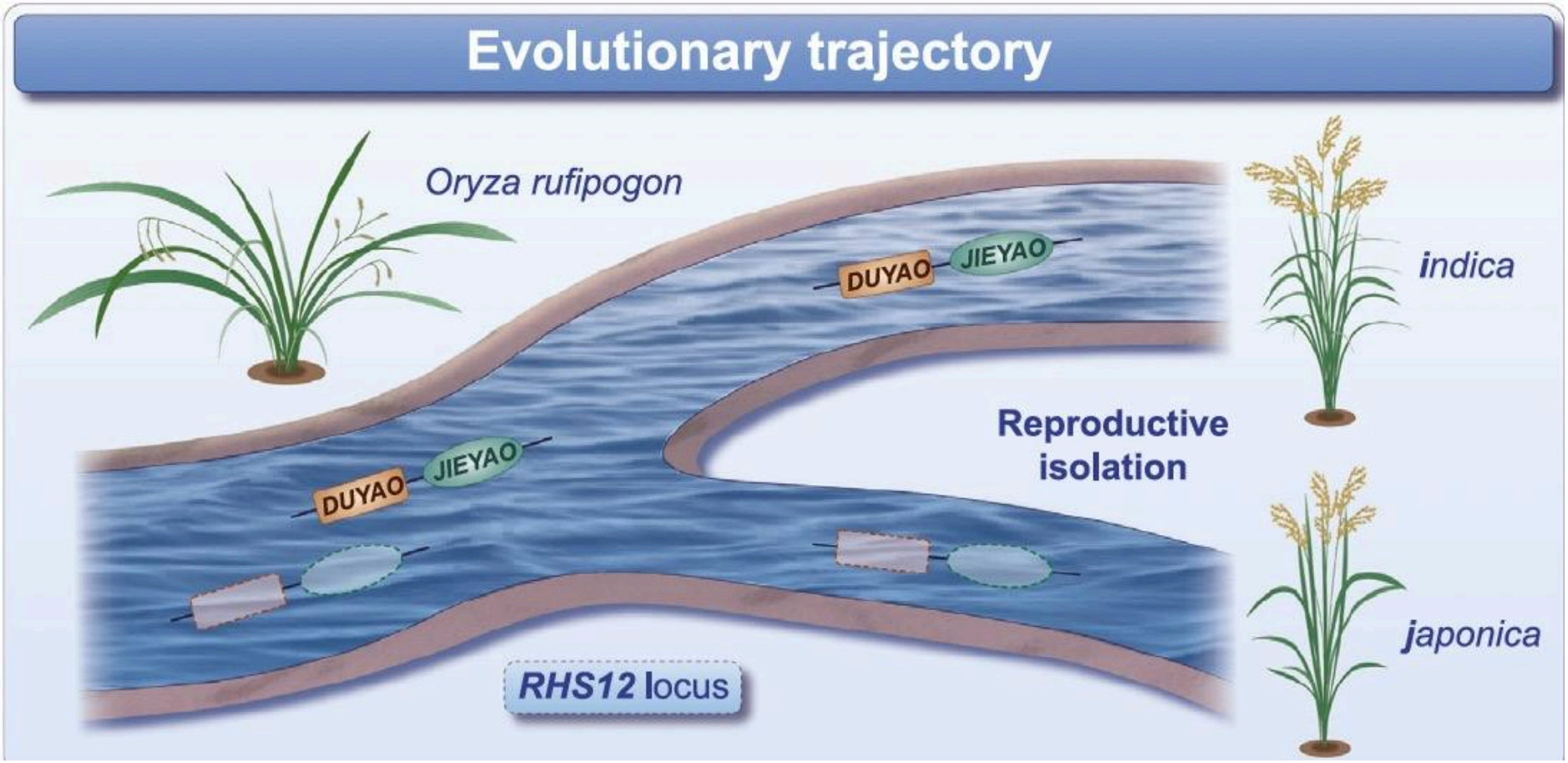



**Figure 7. A proposed working model of the *DUYAO-JIEYAO* element acting as a toxin-antidote system**

(A) The *RHS12* element acts in a sporo-gametophytic interaction manner to control *indica-japonica* hybrid pollen sterility. After meiosis, two types of pollen grains (*RHS12-i* and *RHS12-j*) were produced. The *RHS12-i* pollen is fertile due to detoxification of DUYAO by JIEYAO. The *RHS12-j* pollen is sterile due to lack of JIEYAO. MMC, microspore mother cell.

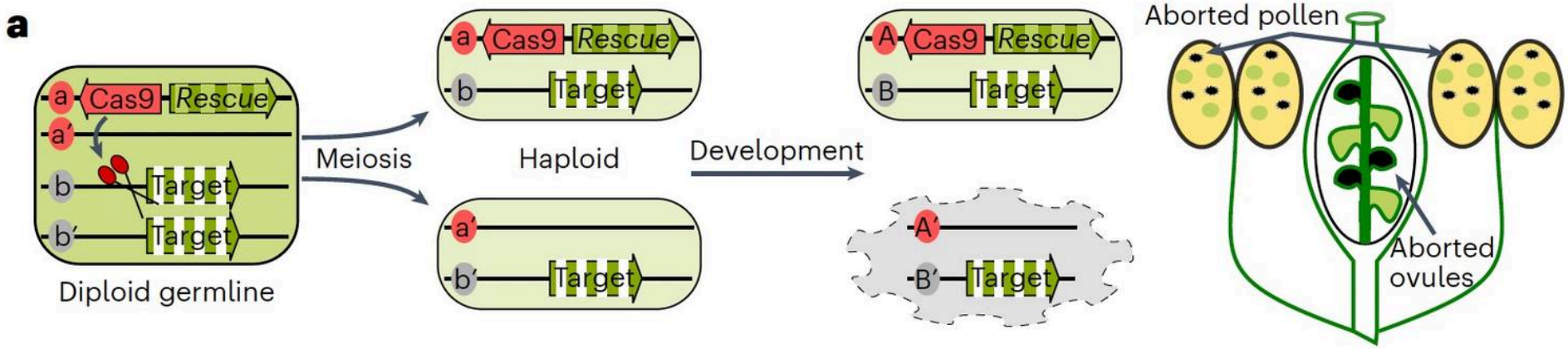
(B) DUYAO acts as a toxin by forming a complex with OsCOX11 and blocking its housekeeping function in mitochondria, thus causing cell death. JIEYAO acts as an antidote to protect cells by interacting with DUYAO and rerouting it to the autophagosome for degradation.

https://doi.org/10.1016/j.cell.2023.06.023


Evolutionary trajectory
Oryza rufipogon
DUYAO
JIEYAO
DUYAO
JIEYAO
Reproductive isolation
indica
japonica
RHS12 locus

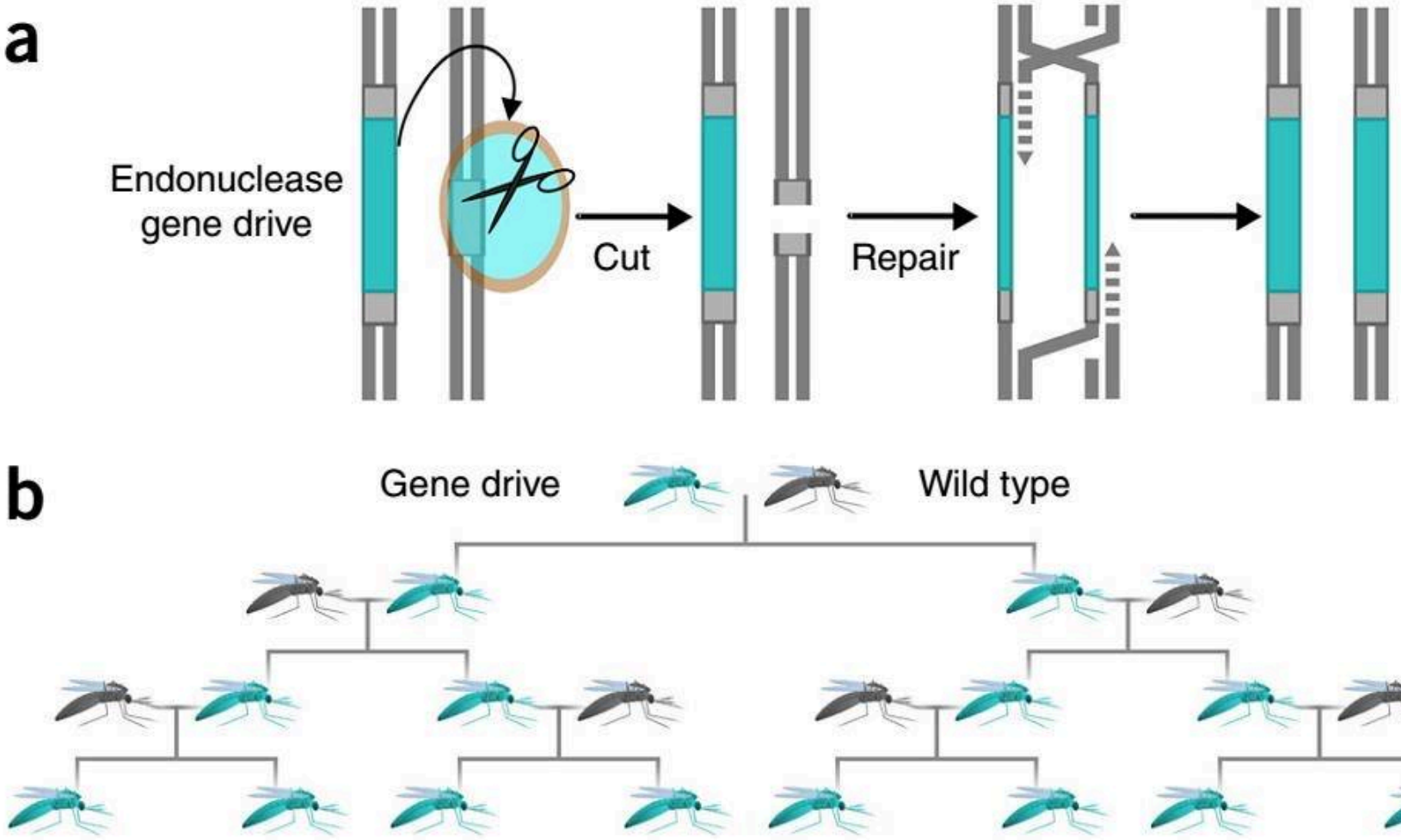
**Cleavage and creation of loss-of-function (lof) alleles in the target (essential gene) occurs before meiosis. In this way both copies of the target gene are rendered non-functional before the first meiotic division segregates the vector-bearing chromosome into one gamete (which survives) and the non-vector-bearing gamete into the other one, which dies.**

**The promoters driving Cas9/gRNA function express during the diploid stage. This can either be in all cells (ubiquitous promoter), tissues that will give rise to the germline or during the diploid stages of meiosis, before the first meiotic division occurs, which separates the homologous chromosomes into haploid gametes**

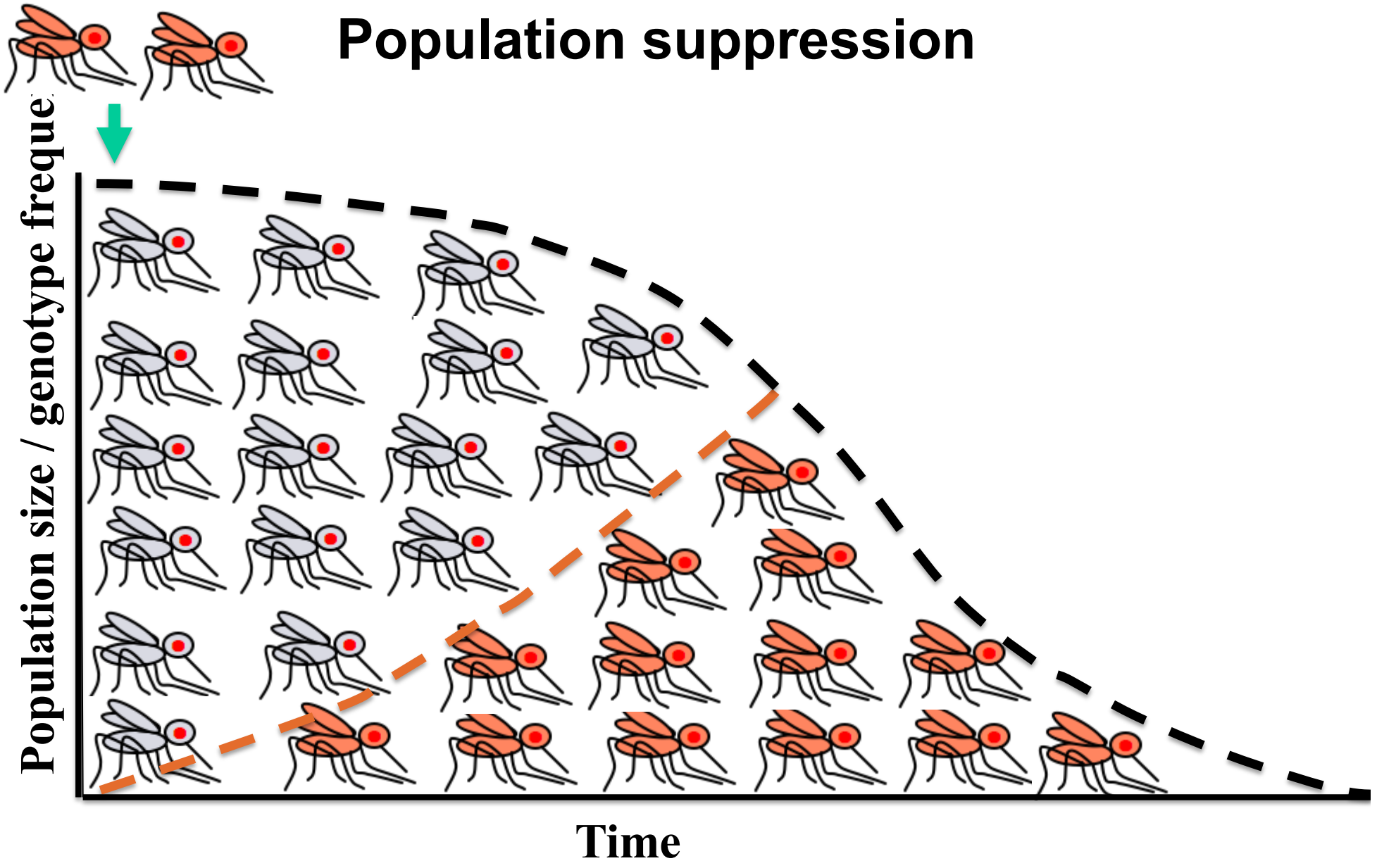


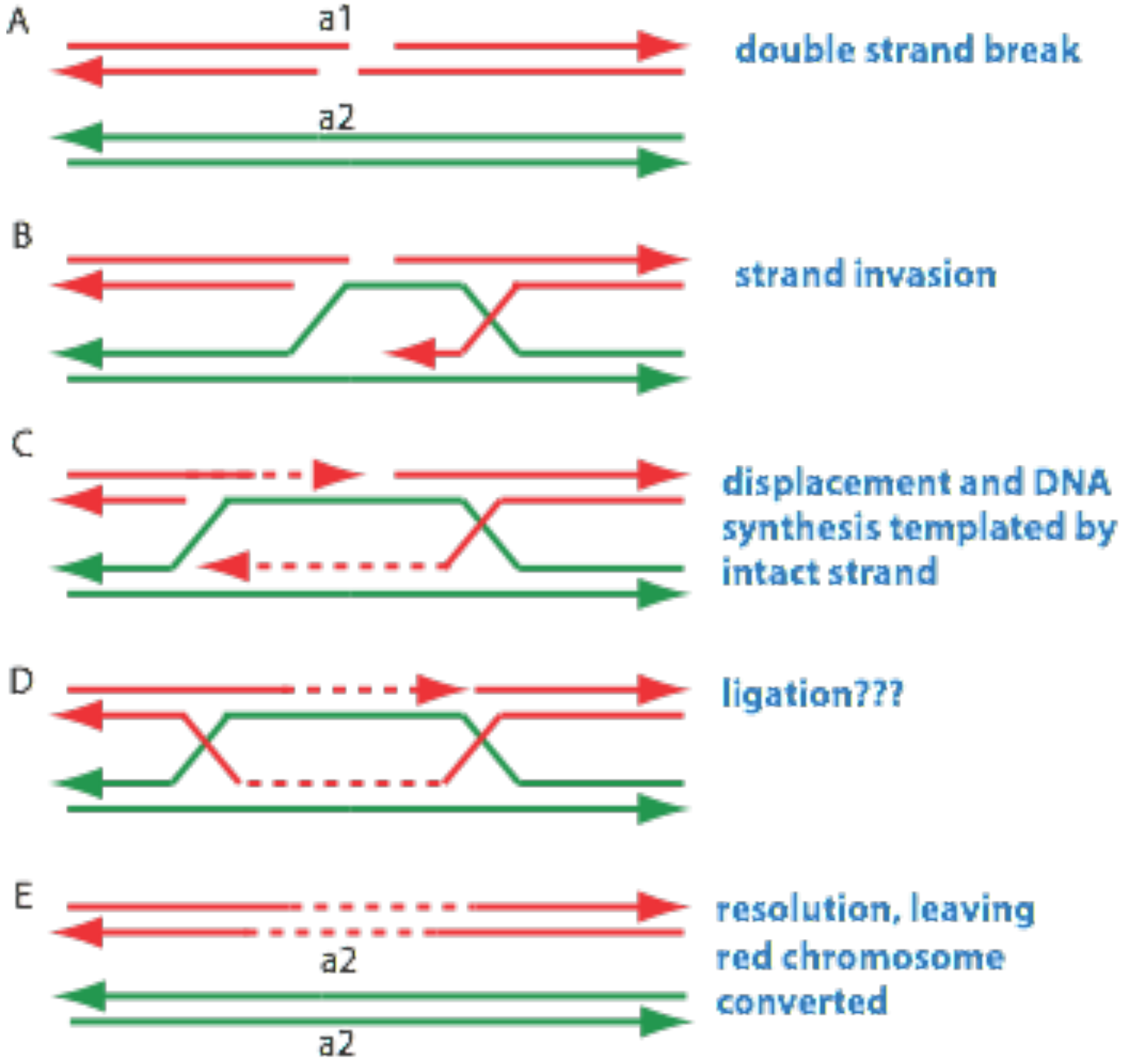

https://doi.org/10.1038/s41477-024-01701-3

**Endonuclease cleaves the homologous chromosome at the site where the endonuclease gene is located. The gene drive element disrupts the target site. Thus, in heterozygotes only the sequence on the WT chromosome gets cleaved. If this break is repaired via HR in the germline then the drive element increases in frequency from 1 to 2.**



# Eliminating a population, at least locally



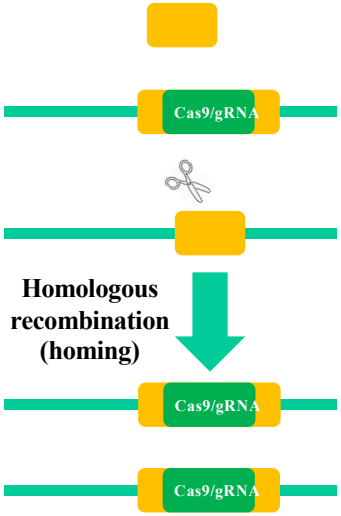

A
a1
a2
double strand break
B
strand invasion
C
displacement and DNA synthesis templated by intact strand
D
ligation???
E
a2
a2
resolution, leaving red chromosome converted

# Over-replication: Homing/gene conversion...and suppression

**A**

**Homologous recombination between two chromosomes, initiated by a DNA break, results in copying**

**Gene required for female fertility/viability**



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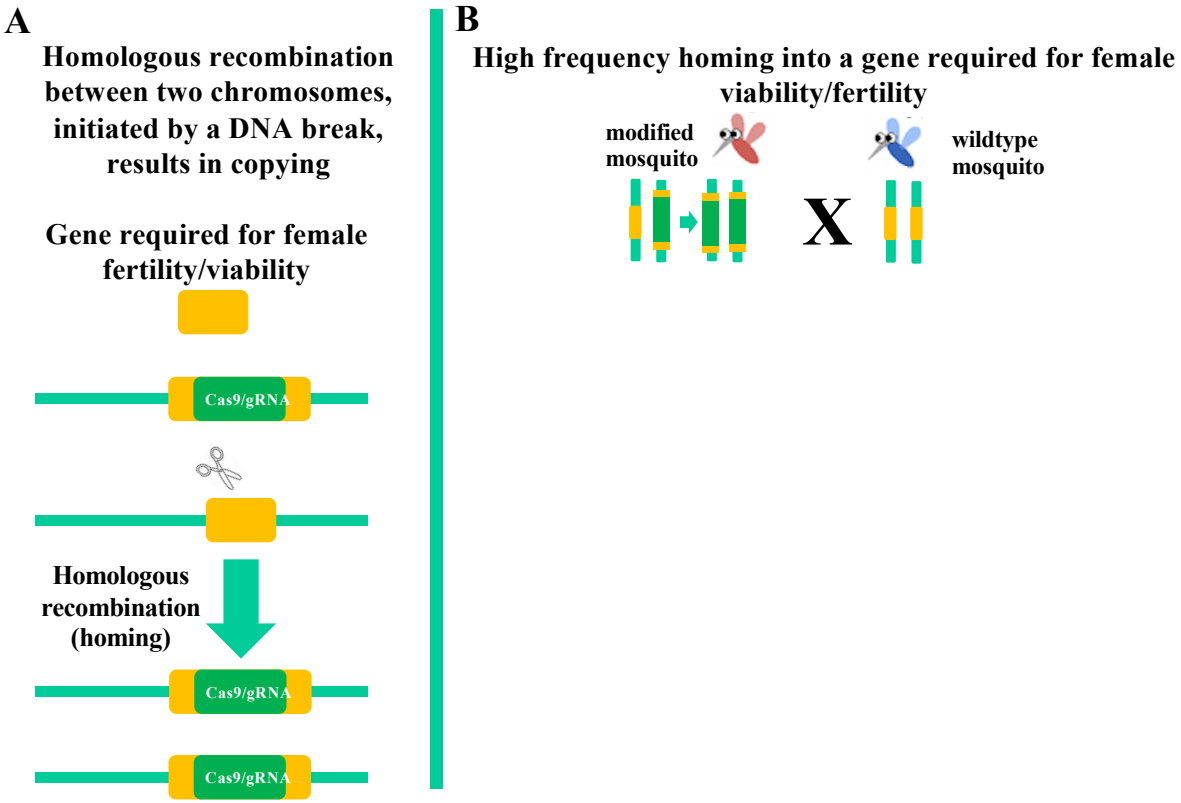

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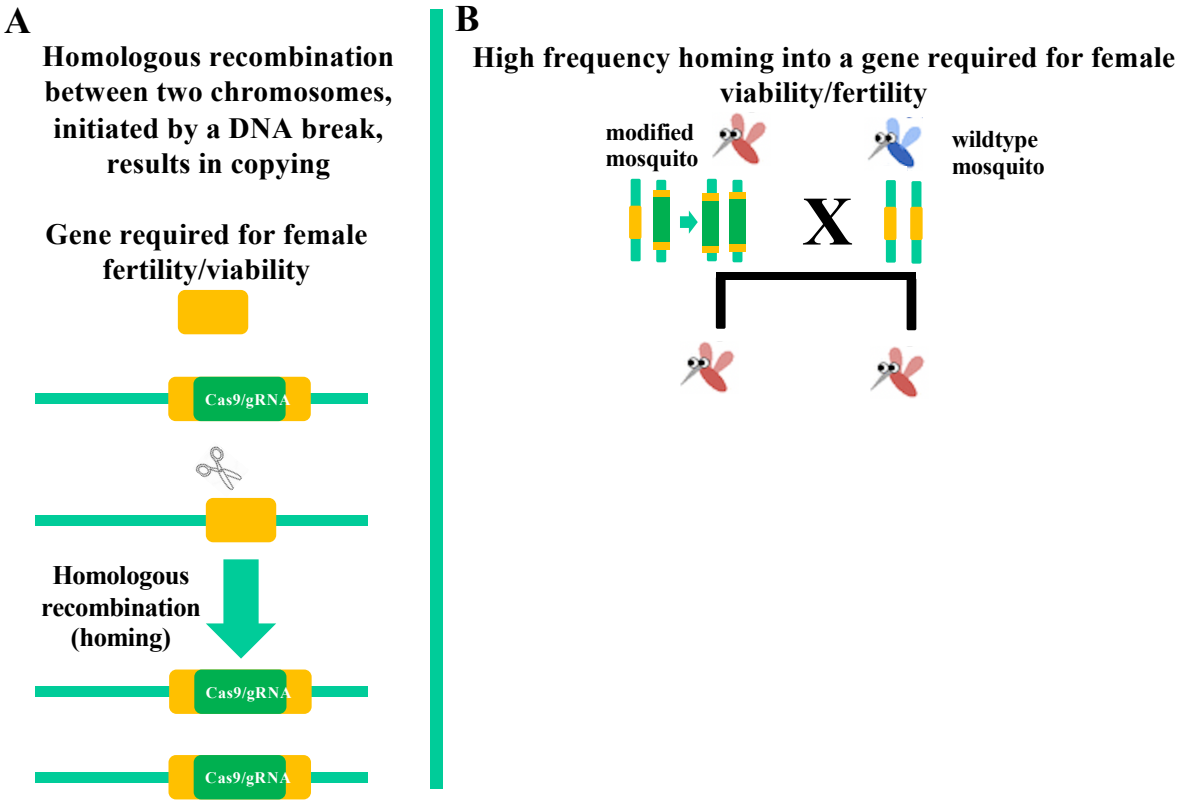

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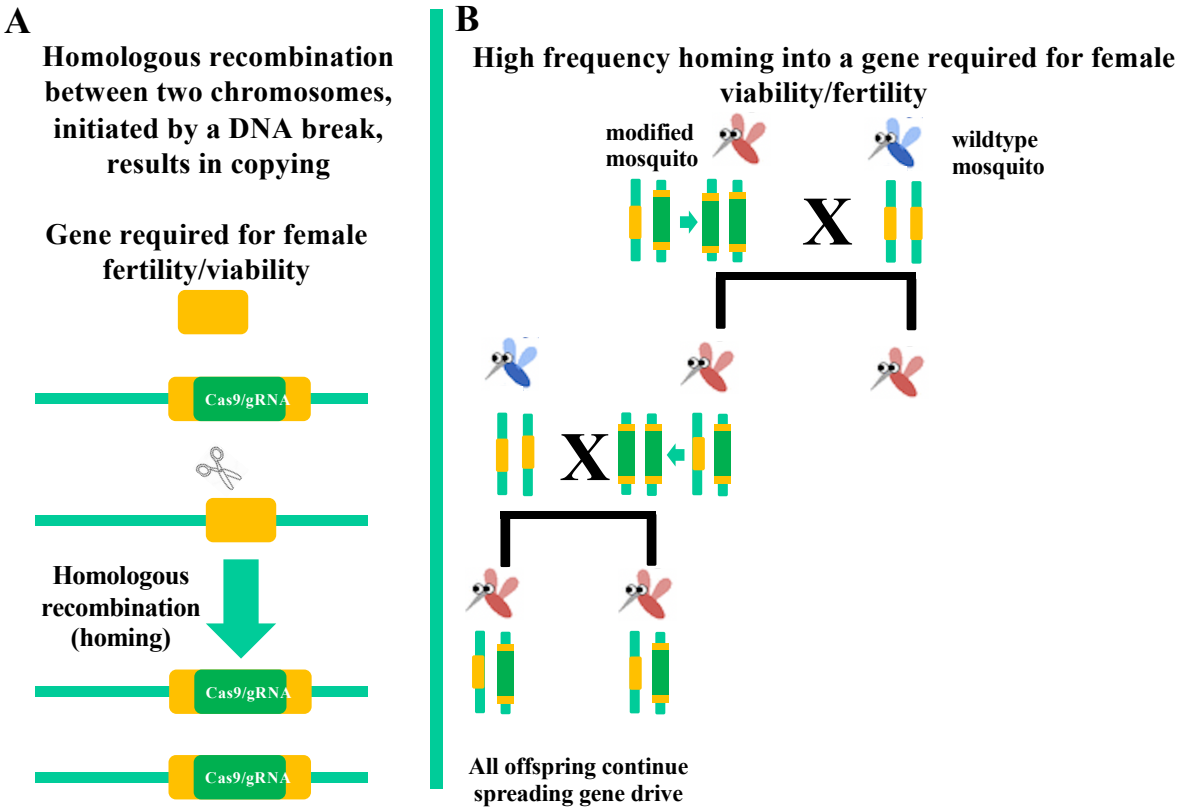

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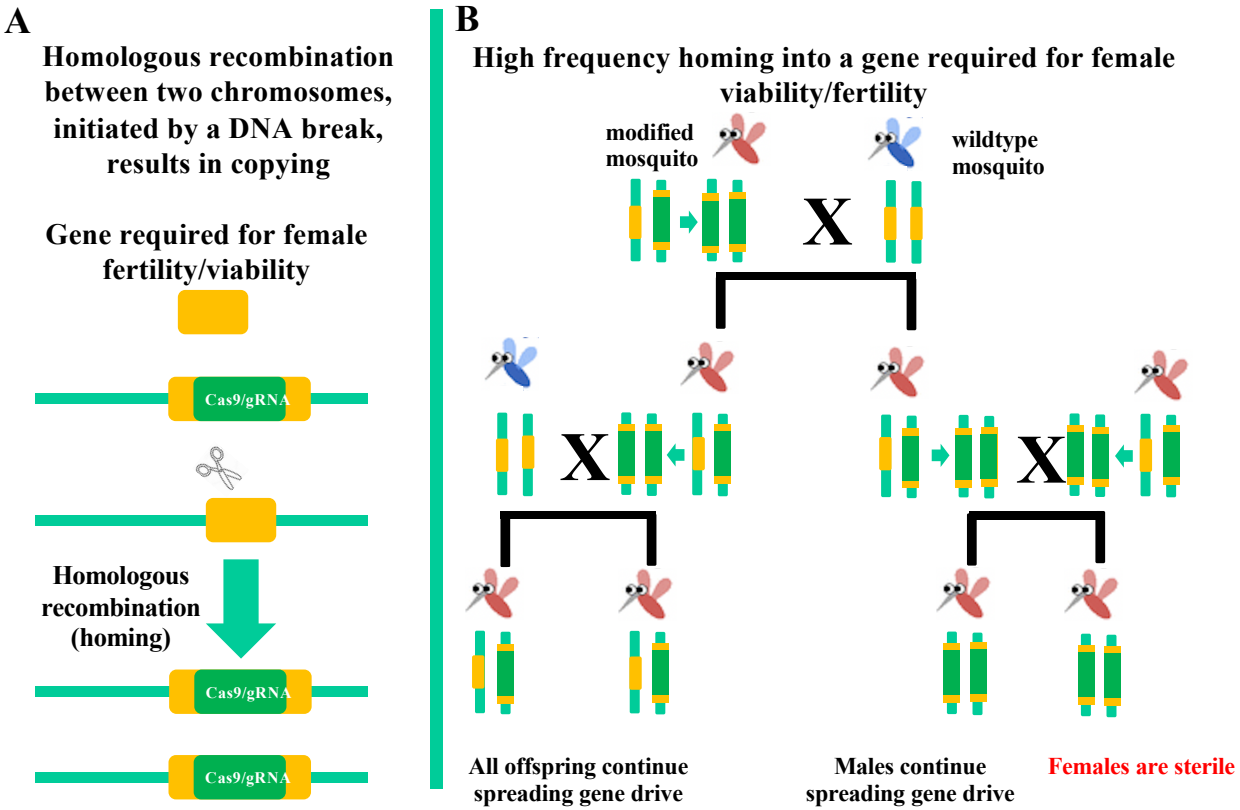

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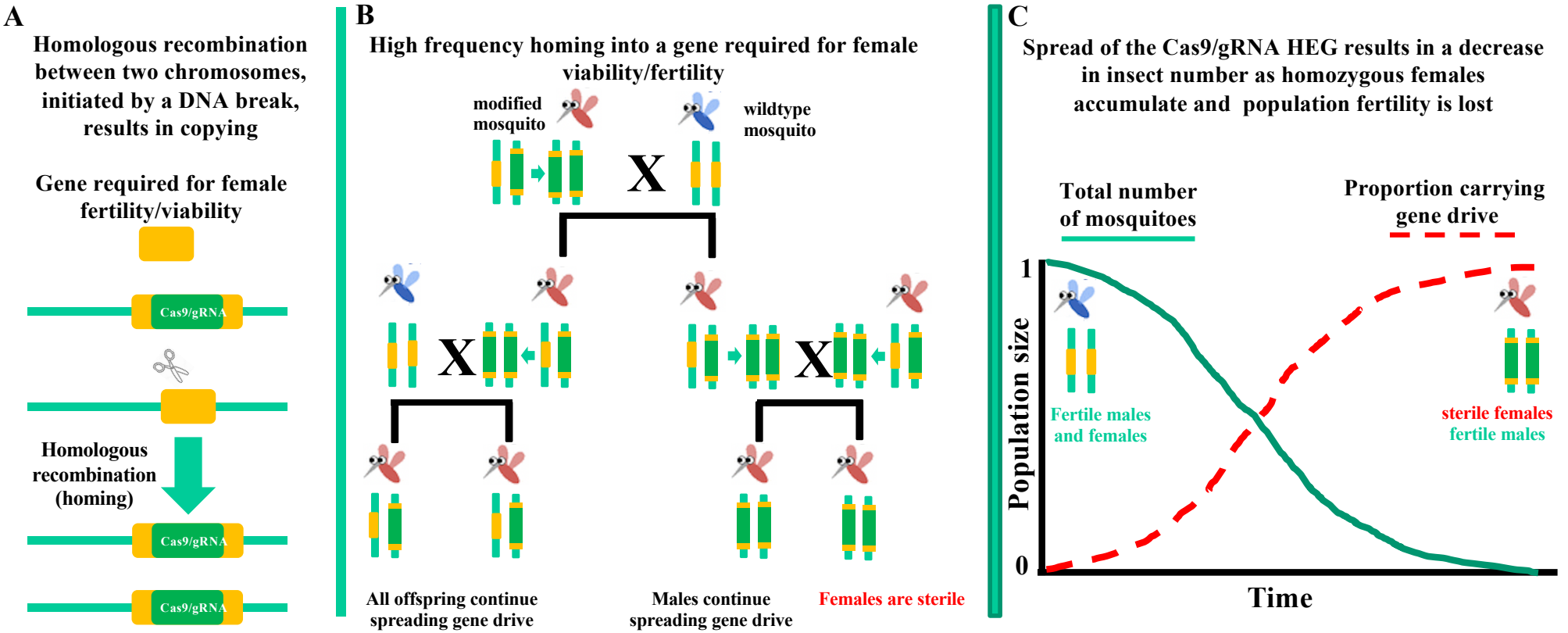
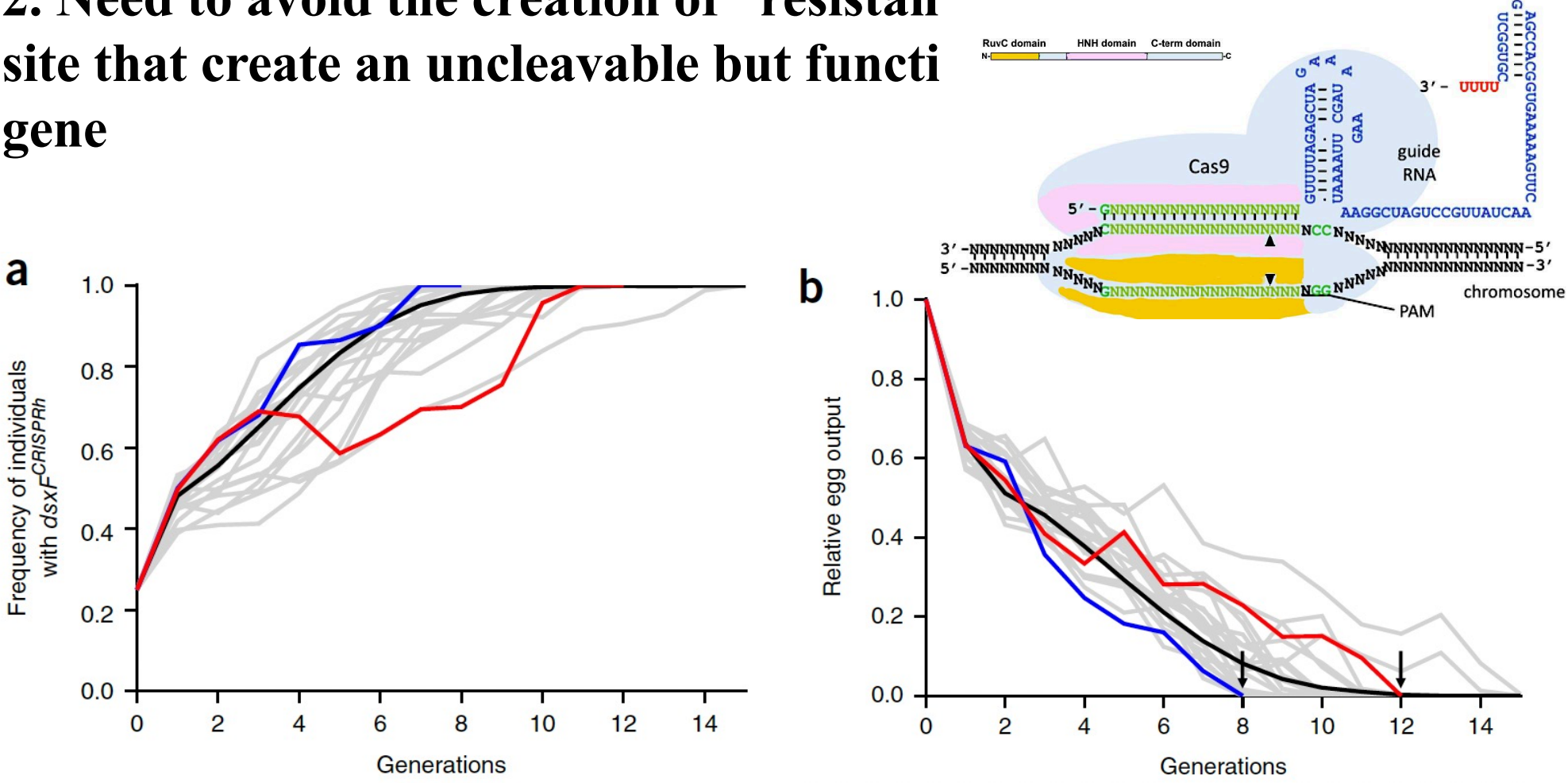
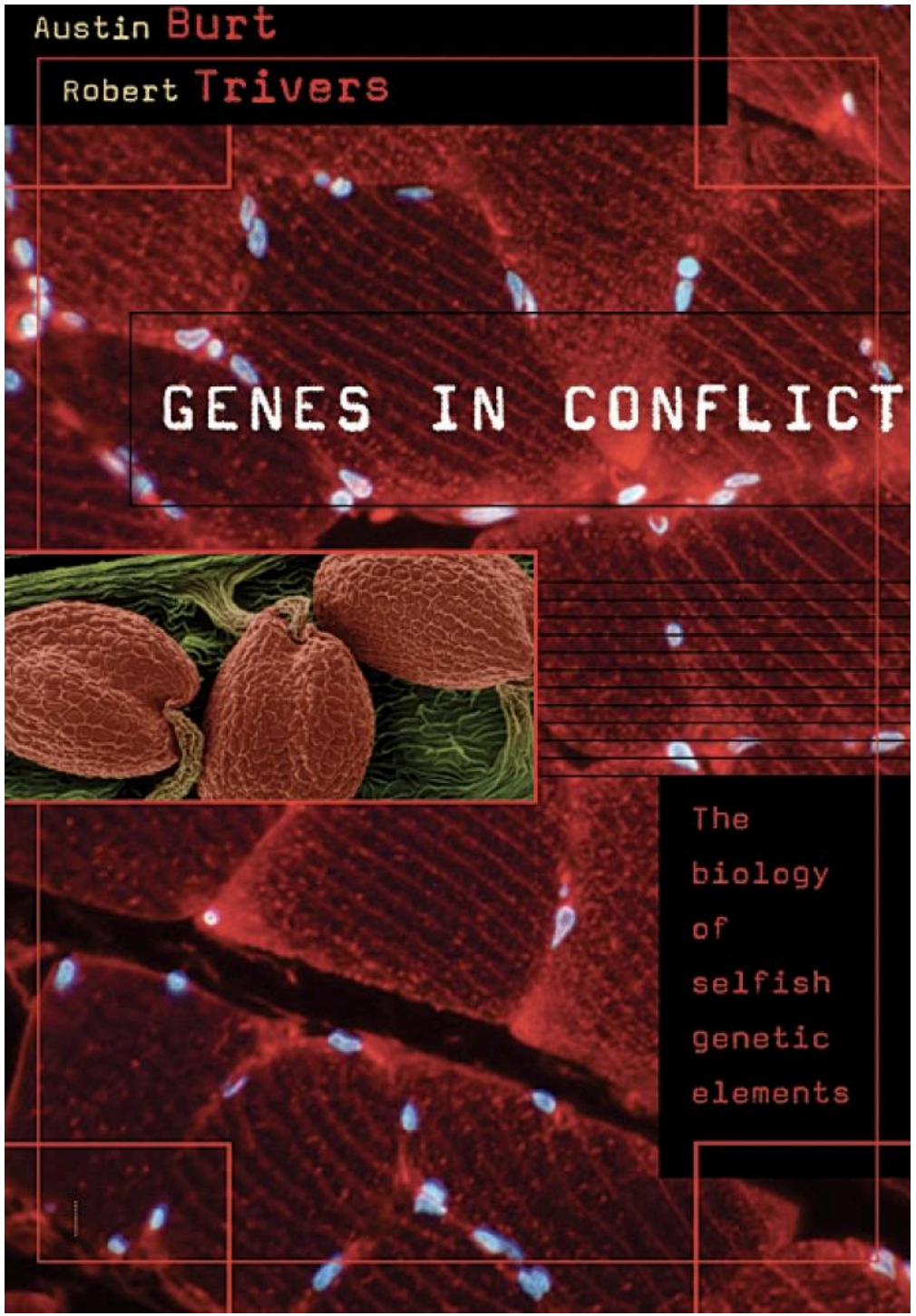


# 1. Requires that homing rates in the germline are very high

# 2. Need to avoid the creation of "resistance" alleles at the target site that create an uncleavable but functi gene




**A CRISPR–Cas9 gene drive targeting doublesex causes complete population suppression in caged Anopheles gambiae mosquitoes.** Nat Biotechnol. 2018 Dec;36(11):1062-1066. doi: 10.1038/nbt.4245. Epub 2018 Sep 24.


Austin Burt
Robert Trivers
GENES IN CONFLICT
The biology of selfish genetic elements

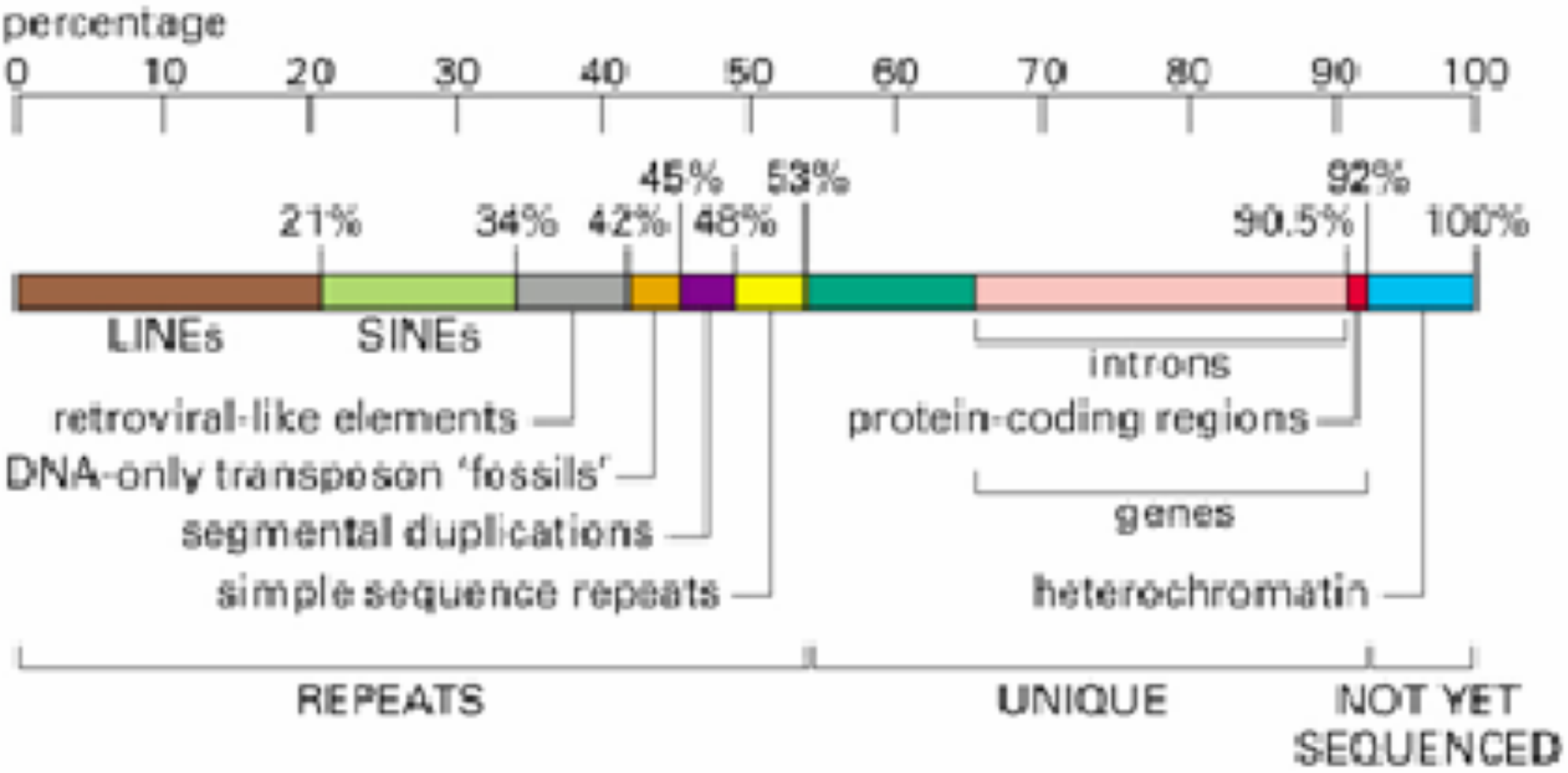



Figure 4–17. Molecular Biology of the Cell, 4th Edition.

**Repetitive DNA sequences in the human genome are the consequences of transposition.**

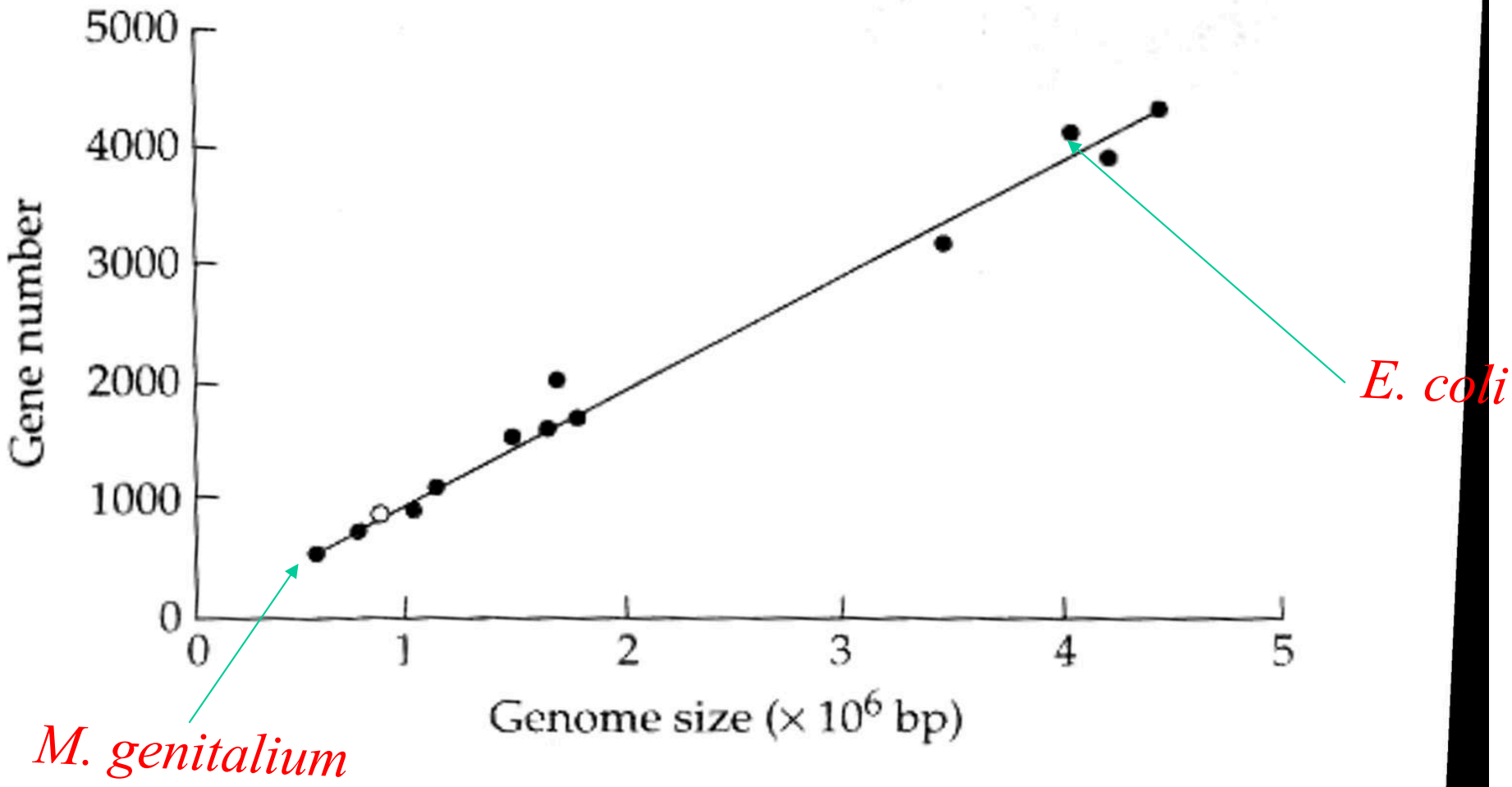
# Range of prokaryotic genome sizes

| | Range in genome size (kb) | Ratio (highest/lowest) |
|---|---|---|
| Eubacteria | 580–13,200 | 20 |
| Mycoplasmas | 580–1,800 | 3 |
| Gram negative | 650–7,800 | 12 |
| Gram positive | 1,600–11,600 | 7 |
| Cyanobacteria | 3,100–13,200 | 4 |
| Archaebacteria | 1,600–4,100 | 3 |

From Cavalier-Smith (1985), updated by knowledge of the *Mycoplasma genitalium* (Fraser et al. 1995).

Graur & Li. Fundamentals of Molecular Evolution (1999)

# Genome size in prokaryotes is correlated with gene number

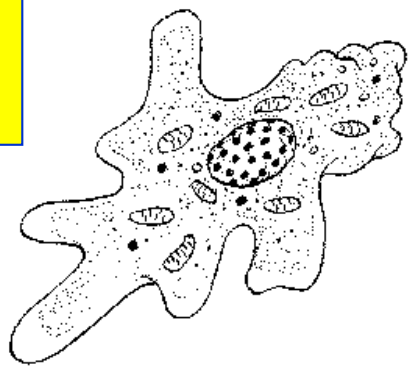



Graur & Li. Fundamentals of Molecular Evolution (1999)

The genome size, or 'C-value', of an organism is defined as the total amount of DNA contained within its haploid chromosome set.

| | (Gb) |
|---|---|
| *H. sapiens* | 2.9 |
| *M. musculus* | 2.5 |
| *D. melanogaster* | 0.18 |
| *C. elegans* | 0.097 |
| *S. cerevisiae* | 0.012 |


the single-celled amoeba, one of the simplest of eukaryotic creatures, has a genome size of ~200,000 Mb!



# The range of genome sizes in various eukaryotic groups

| *Taxon* | *Genome size range (Kb)* | *Ratio* |
|---|---|---|
| All eukaryotes | 8,800–686,000,000 | 77,955 |
| Alveolata | 23,500–201,000,000 | 8,553 |
| Apicomplexians | 9,400–201,000,000 | 21,383 |
| Ciliates | 23,500–8,620,000 | 367 |
| Dinoflagellates | 1,370,000–98,000,000 | 72 |
| Diatoms | 35,300–24,500,000 | 694 |
| Amoebae | 35,300–686,000,000 | 19,433 |
| Euglenozoa | 98,000–2,350,000 | 24 |
| Fungi | 8,800–1,470,000 | 167 |
| Animals | 49,000–139,000,000 | 2,837 |
| Sponges | 49,000–53,900 | 1 |
| Cnidarians | 323,000–715,000 | 2 |
| Aschelminthes | 80,000–2,450,000 | 31 |
| Annelids | 882,000–5,190,000 | 6 |
| Mollusks | 421,000–5,290,000 | 13 |
| Crustaceans | 686,000–22,100,000 | 32 |
| Insects | 98,000–7,350,000 | 75 |
| Echinoderms | 529,000–3,230,000 | 6 |
| Non-vertebrate chordates | 157,000–1,470,000 | 9 |
| Agnathes | 637,000–2,790,000 | 4 |
| Elasmobranchs | 1,470,000–15,800,000 | 11 |
| Bony fishes | 340,000–139,000,000 | 409 |
| Amphibians | 931,000–84,300,000 | 91 |
| Reptiles | 1,230,000–5,340,000 | 4 |
| Birds | 1,670,000–2,250,000 | 1 |
| Mammals | 1,700,000–6,700,000 | 4 |
| Monotremes | 3,470,000–3,700,000 | 1 |
| Marsupials | 3,470,000–4,560,000 | 1 |
| Placentals | 1,700,000–6,700,000 | 4 |
| Plants | 50,000–307,000,000 | 6,140 |
| Algae | 80,000–30,000,000 | 375 |
| Pteridophytes | 98,000–307,000,000 | 3,133 |
| Gymnosperms | 4,120,000–76,900,000 | 17 |
| Angiosperms | 50,000–125,000,000 | 2,500 |

Eukaryotes vary over a range of 80,000!

Graur & Li. Fundamentals of Molecular Evolution (1999)

# The C-value paradox:

*What accounts for the often massive, counter-intuitive and seemingly arbitrary differences in genome size observed among eukaryotic organisms?*

The fruit fly
*Drosophila melanogaster*

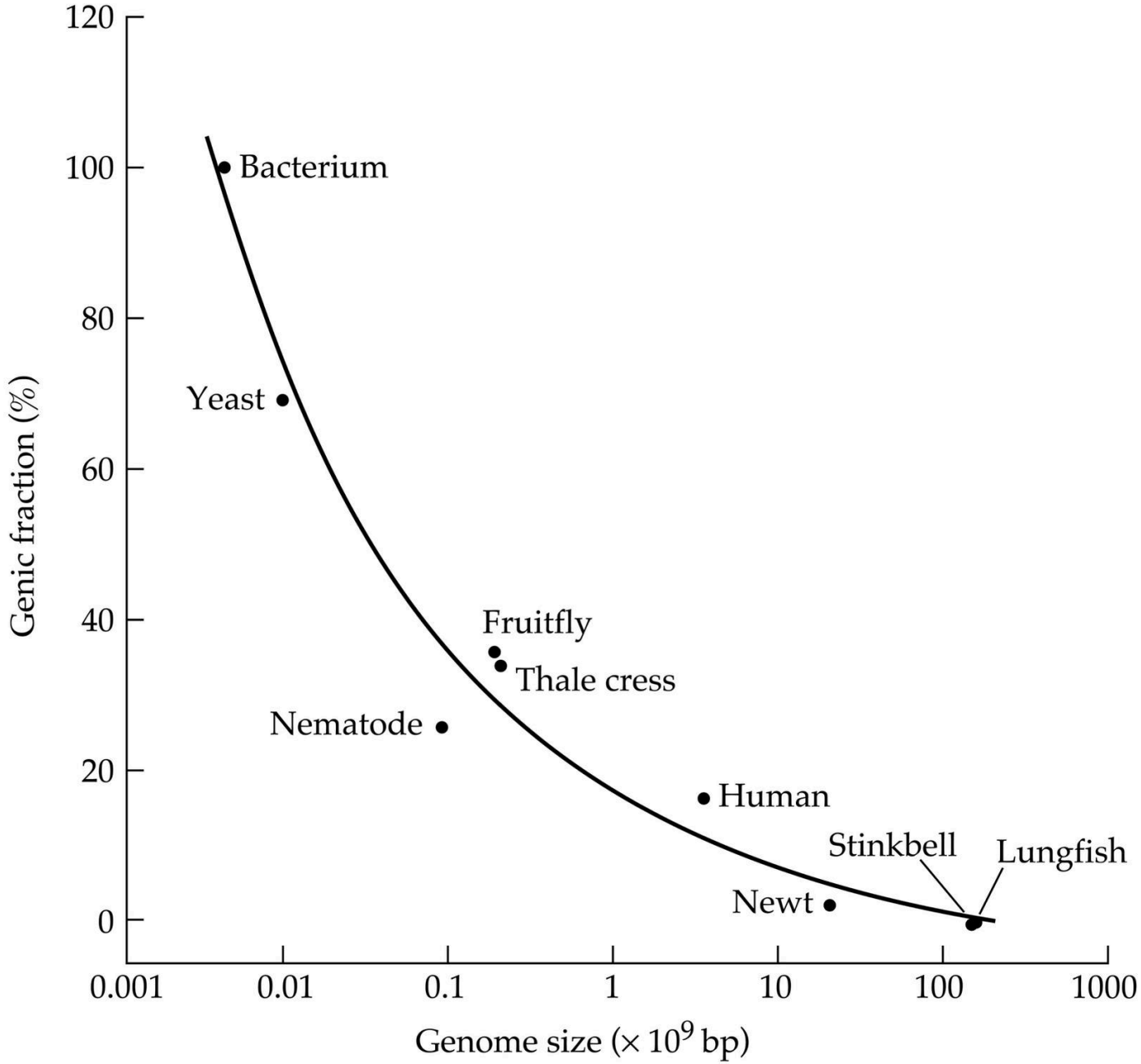
180 Mb

The mountain grasshopper
*Podisma pedestris*

18,000 Mb

The difference in genome size of a factor of 100 is difficult to explain in view of the apparently similar levels of evolutionary, developmental and behavioral complexity of these organisms.

# The key to the C-value paradox lies in the nongenic regions



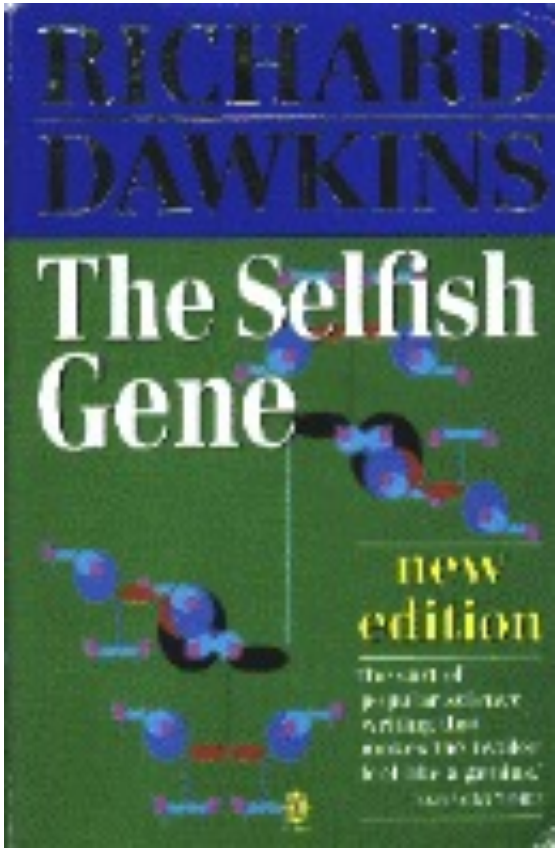
A chicken is just an egg's way of making more eggs

**The gene view of evolution:**
**genes are the basic units of evolution**

"Individuals are not stable things, they are fleeting. Chromosomes too are shuffled to oblivion, like hands of cards soon after they are dealt. But the cards themselves survive the shuffling. The cards are the genes. The genes are not destroyed by crossing-over, they merely change partners and march on. Of course they march on. That is their business. They are the replicators and we are their survival machines. When we have served our purpose we are cast aside. But genes are denizens of geological time: genes are forever."

*The Selfish Gene*
Richard Dawkins

*The Selfish Gene*
Richard Dawkins



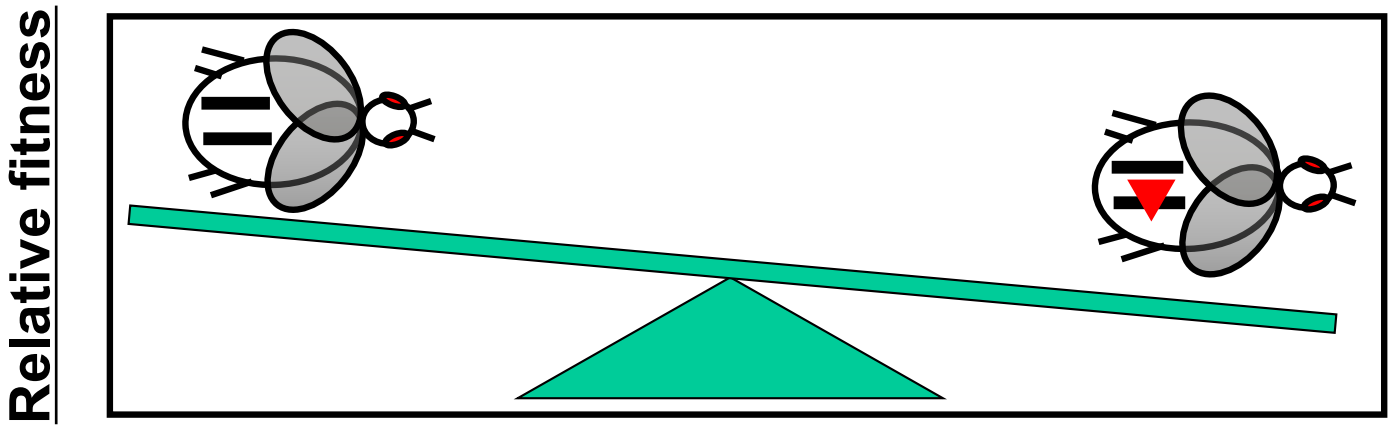

**genes are dynamic entities directly subject to evolutionary forces**

"Genes are competing directly with their alleles for survival, since their alleles in the gene pool are rivals for their slot on the chromosomes of future generations. Any gene that behaves in such a way as to increase its own survival chances in the gene pool at the expense of its alleles will, by definition, tautologously, tend to survive. The gene is the basic unit of selfishness."

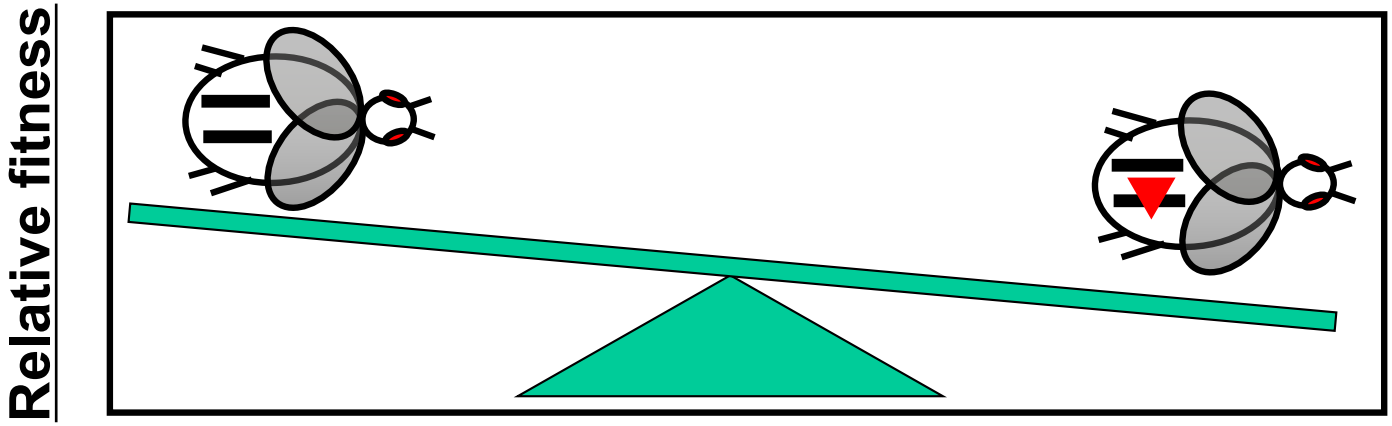
*The Selfish Gene*
Richard Dawkins

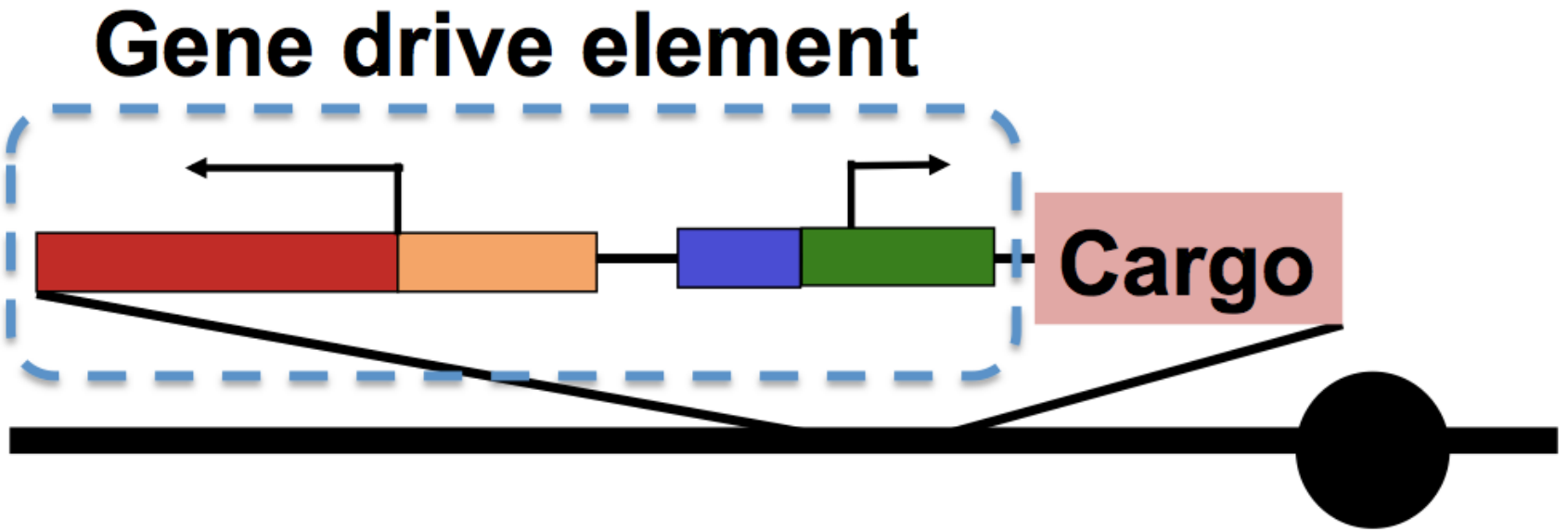
"…it appears that the amount of DNA in organisms is more than is strictly necessary for building them: a large fraction of the DNA is never translated into protein. From this point of view of the individual organism this seems paradoxical. As the 'purpose' of DNA is to supervise the building of bodies, it is surprising to find a large quantity of DNA which does no such thing. Biologists are racking their brains to think what this surplus DNA is doing. But from the point of view of the selfish genes themselves, there is no paradox. The true 'purpose' of DNA is to survive, no more and no less. The simplest way to explain the surplus DNA is to suppose that it is a parasite, or at best a harmless but useless passenger, hitching a ride in the survival machines created by the other DNA." pg 156

# Problem: traits of interest usually result In some fitness cost to carriers

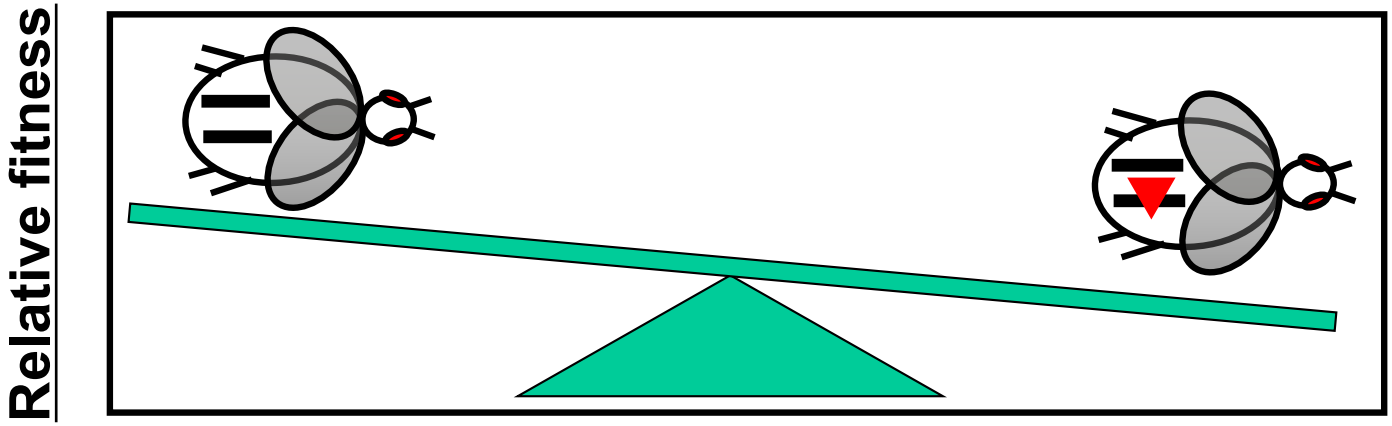


# Problem: traits of interest usually result In some fitness cost to carriers



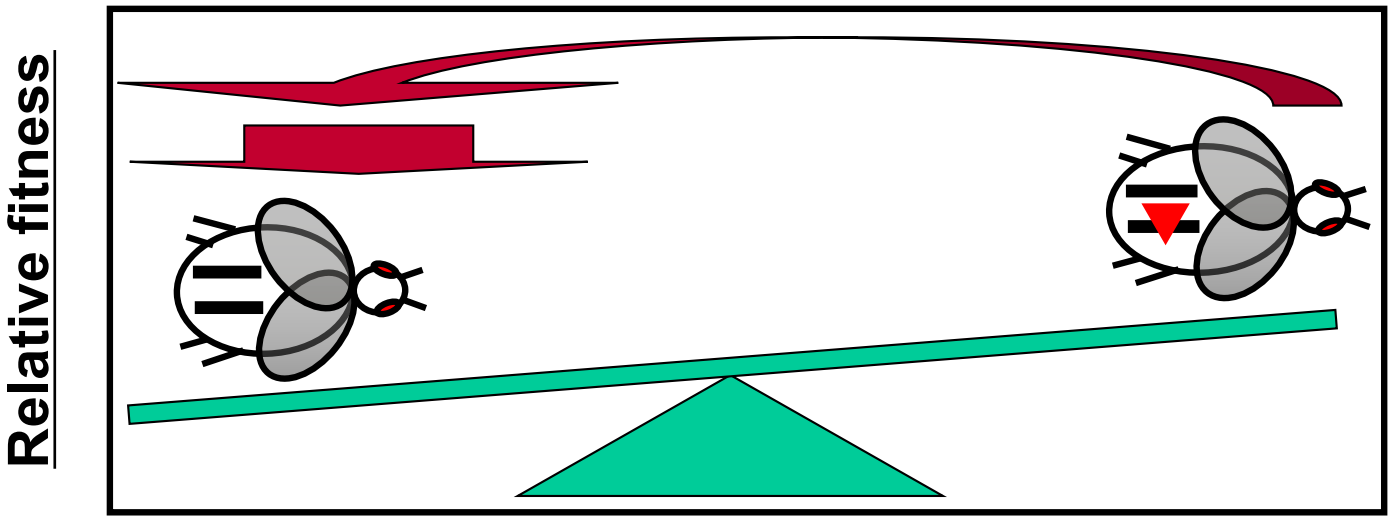



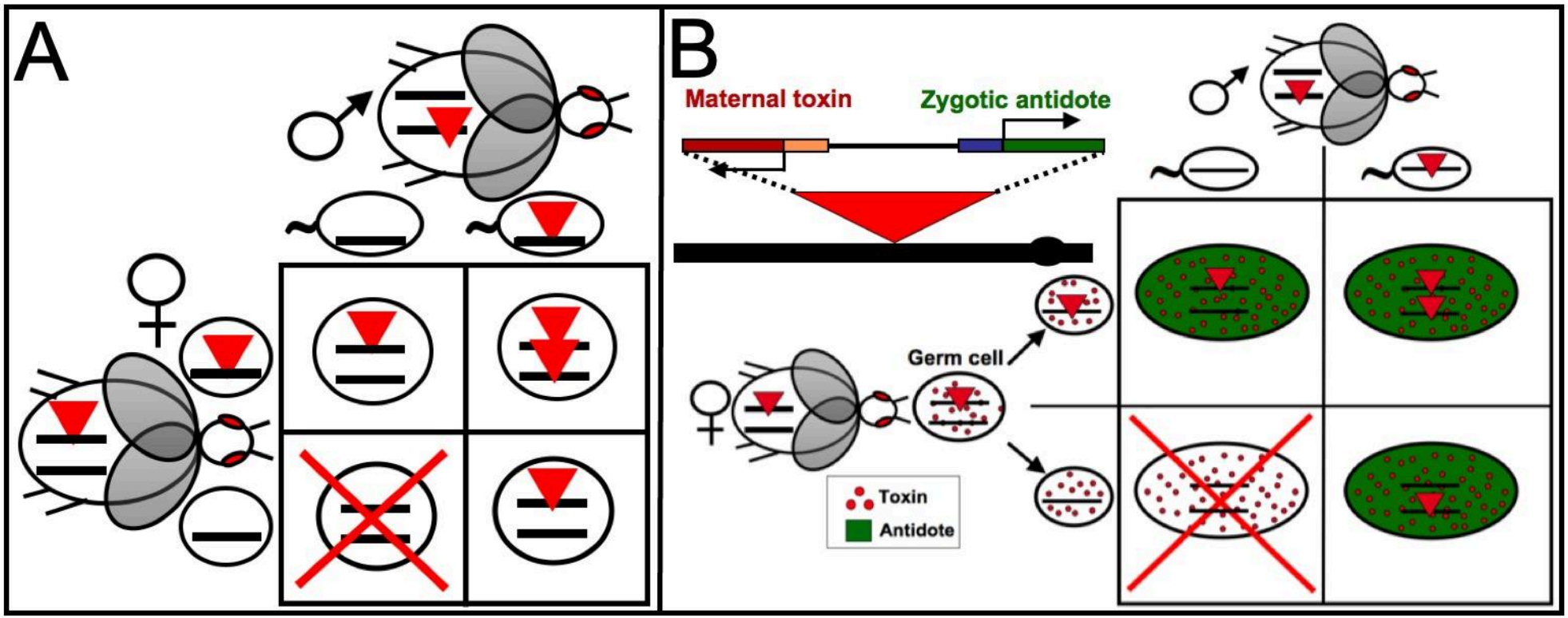
**Problem: traits of interest usually result In some fitness cost to carriers**



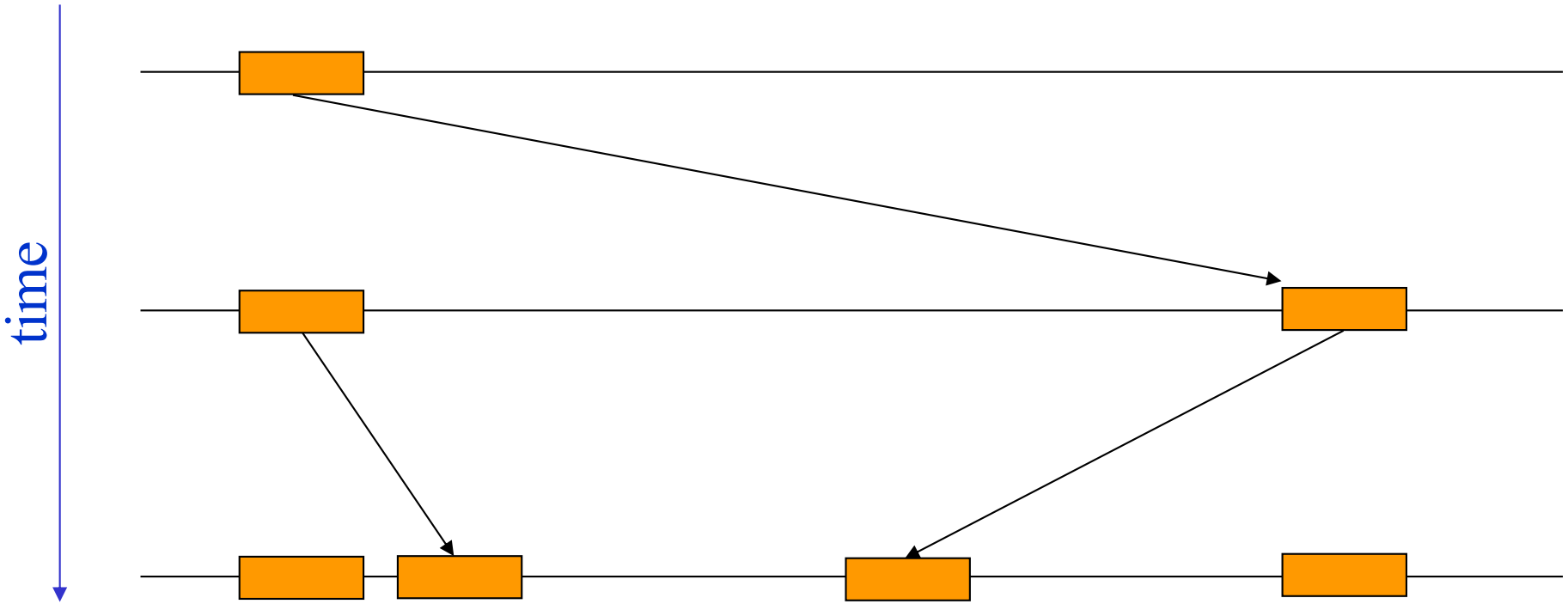

**Solution: Increase the fitness cost associated with NOT carrying the gene of interest**

Gene drive




A
B
Maternal toxin
Zygotic antidote
Germ cell
Toxin
Antidote

Imagine a gene that could duplicate copies of itself within the genome



**A piece of selfish DNA has two distinct properties:**

- Arises when DNA sequence spreads by forming additional copies of itself within the genome
- Makes no specific contribution to the phenotype

"Selfish sequences spread and make no contribution to the phenotype of the organism, except in insofar as it is a slight burden to the cell that contains it. The spread of DNA sequences within the genome can be compared to the spread of a not-too-harmful parasite within its host."

## Intra-genomic selection

"The idea of selfish DNA is firmly based on this general theory of natural selection, but it deals with selection in an unfamiliar context"

"In short, we may expect a kind of molecular struggle for existence within the DNA of the chromosomes, using the process of natural selection.

Orgel, L. E. & Crick, F. H. C. 1980. Nature 284: 604-607

| Structure | Key Genes | Mode of Movement |
| --- | --- | --- |
|  Short inverted repeats at each end | Transposase | Moves as DNA by excision or replication |
|  Long direct repeats at both ends | Reverse Transcriptase Integrase | Moves by a RNA intermediate |
|   Poly-A at 3' end 5' end often truncated | Reverse Transcriptase/ Endonuclease | Moves by a RNA intermediate |

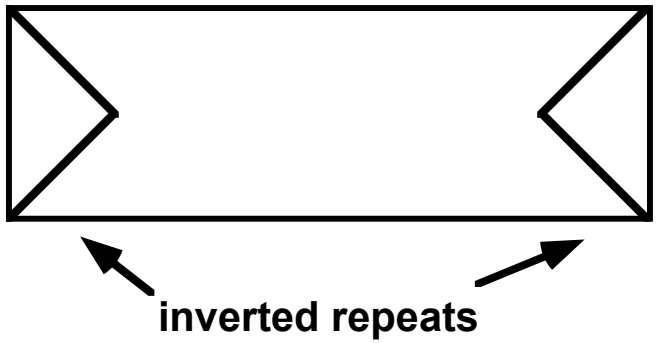
# Bacterial transposons  Insertion (IS) sequences

**What defines most transposons**

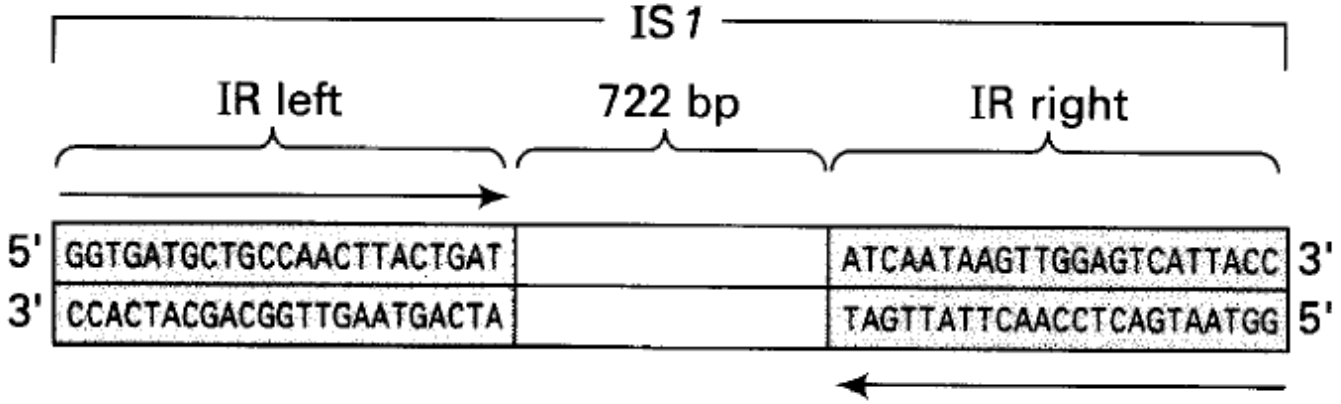
1. Inverted repeats
2. Sequences between the inverted repeats that may be transported
3. A source of transposase, and in the case of replicative transposition, a source of resolvase.
   Transposase provides a mechanism to move these elements from one site to another.

## The basic prokaryotic unit of transposon unit is an IS and a source of transposase.

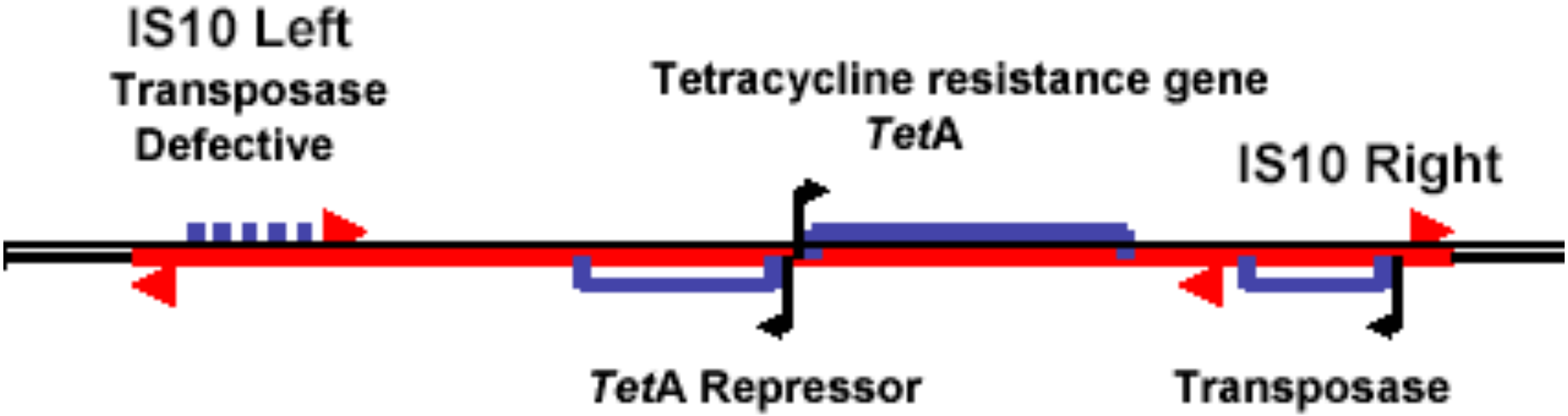
**Insertion sequence**




Transposase may be provided either in cis (between the inverted repeats) or in trans (somewhere else on the bacterial chromosome).

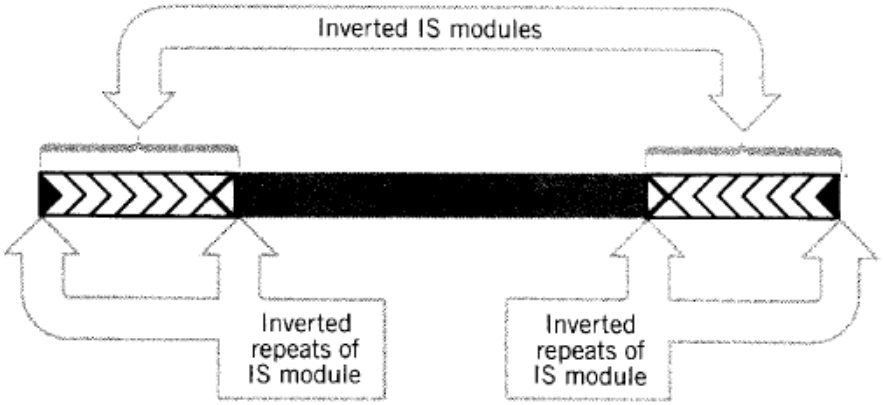


# Structure of a Complex Transposon Tn10




IS10 Right may transpose by itself
or Tn10 can be moved as a unit

# A composite transposon has a central region carrying markers (genes) unconnected with transposition, flanked by IS modules.



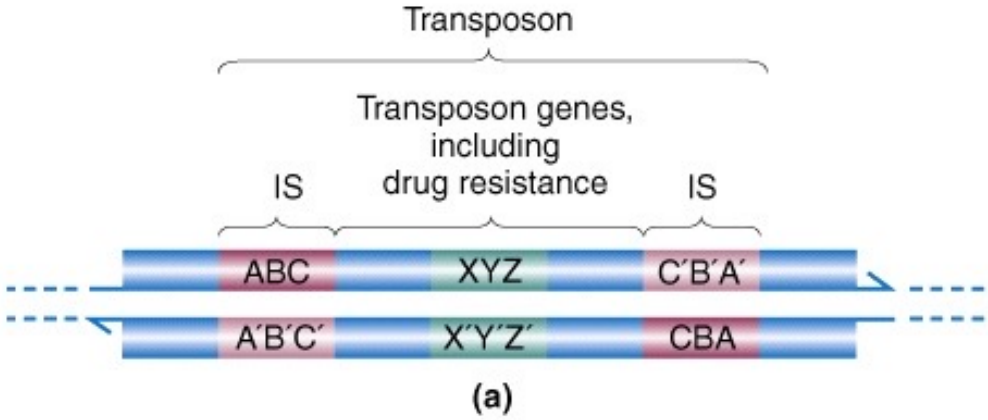
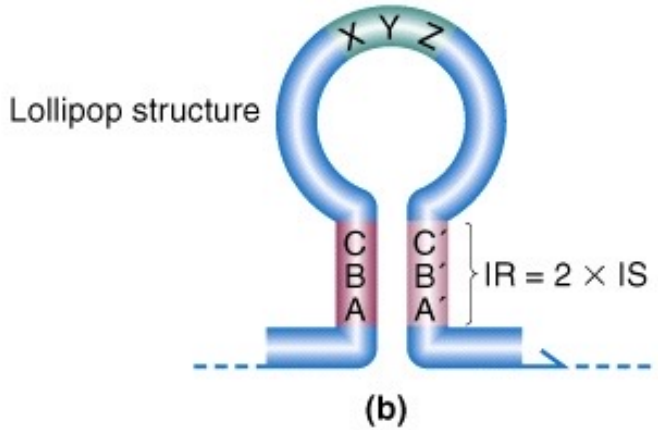
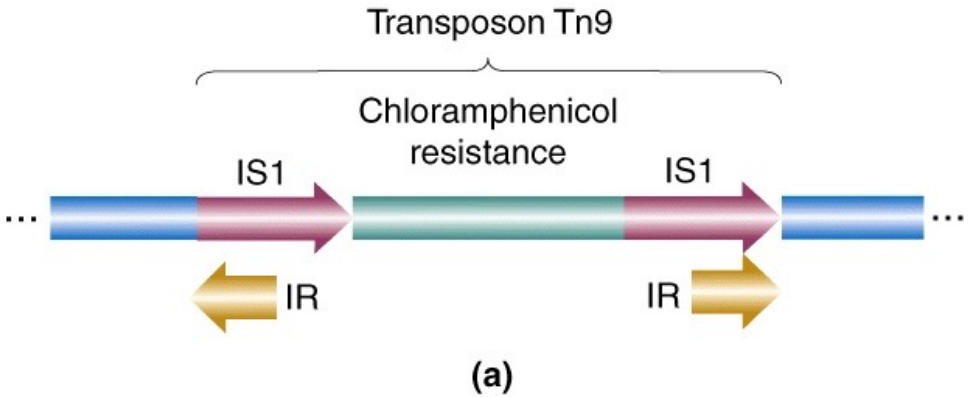
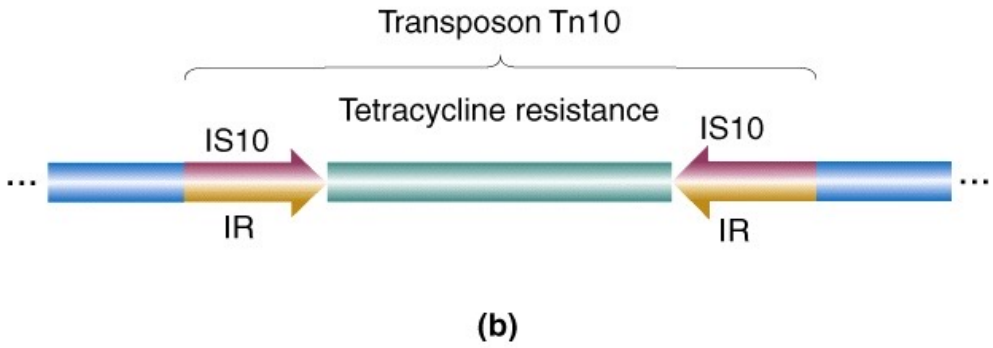



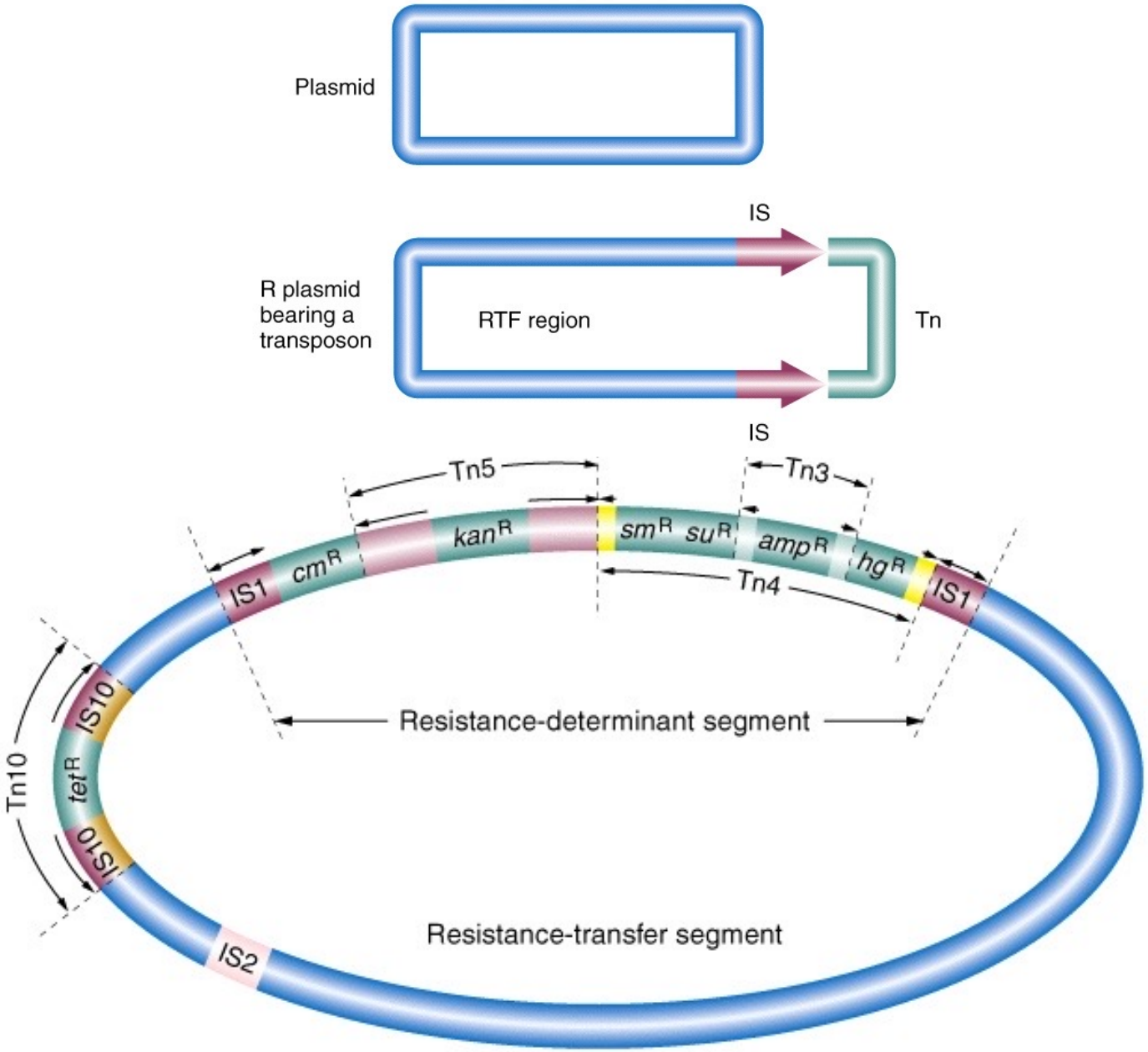

**Figure 35.3**
**A composite transposon has a central region carrying markers unconnected with transposition (such as drug resistance) flanked by IS modules. The modules have short inverted terminal repeats. If the modules themselves are in inverted orientation (as drawn), the short inverted terminal repeats at the ends of the transposon are identical.**



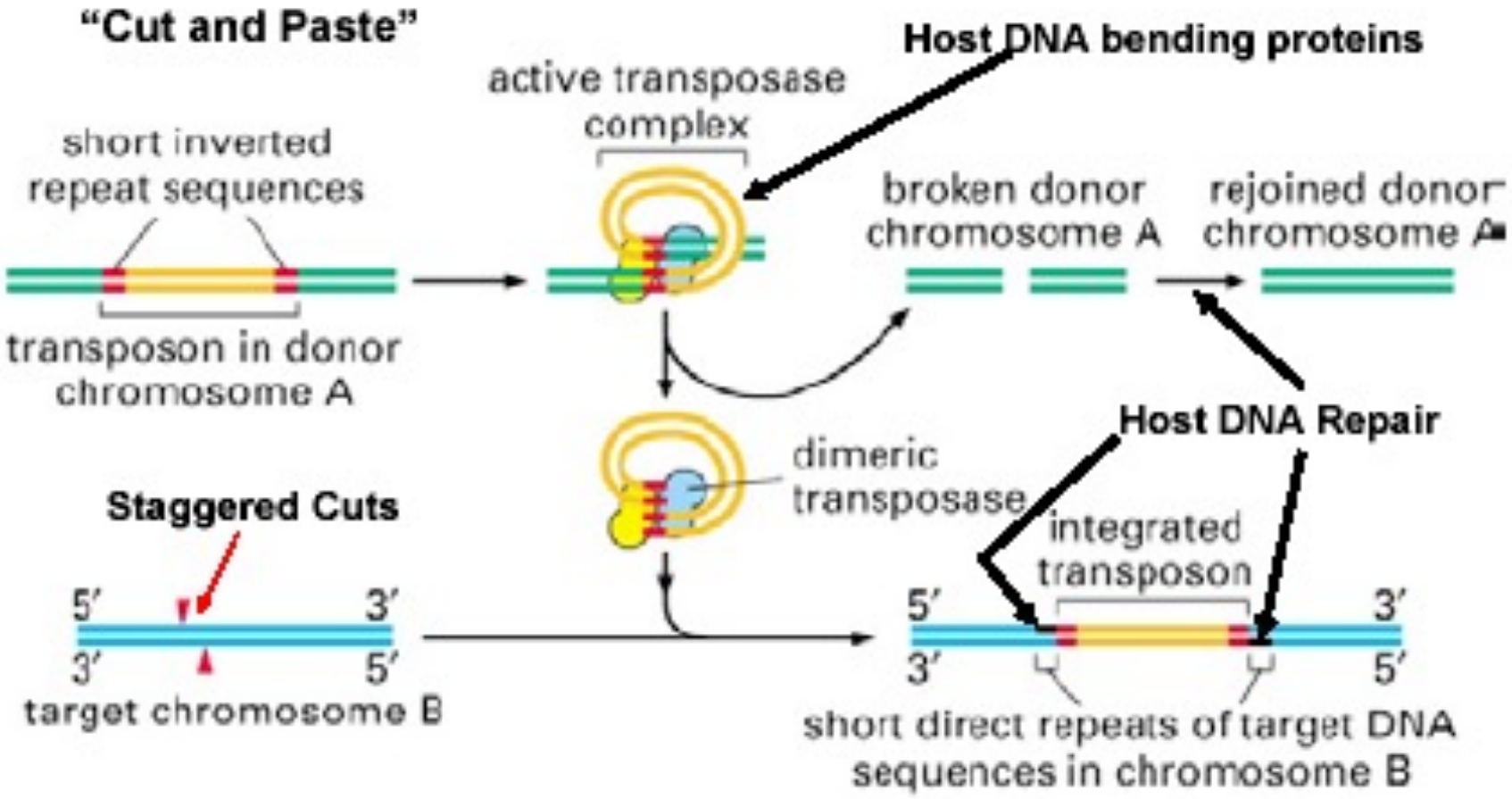



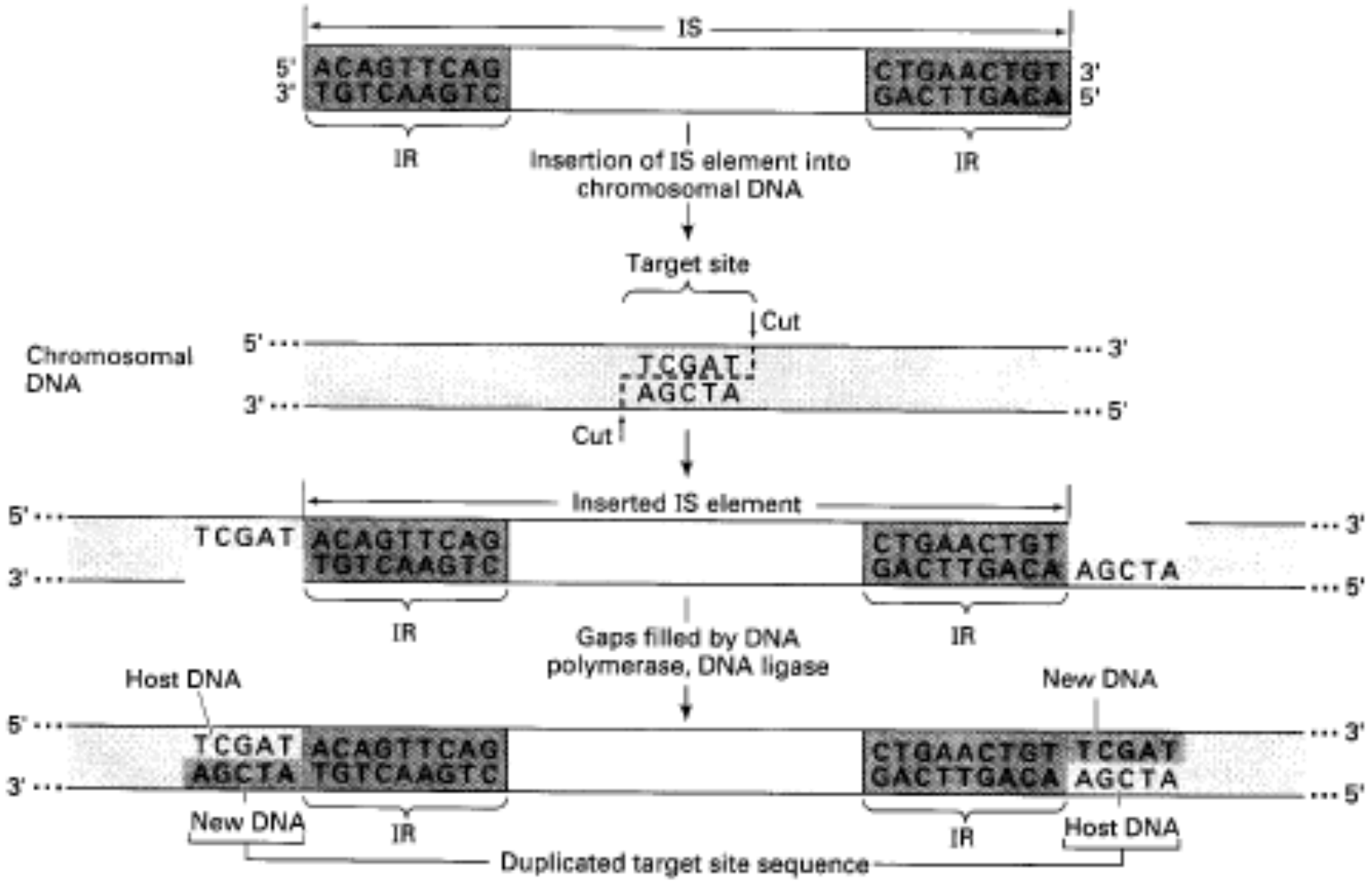
**Plasmids are autonomously replicating elements located in the bacterial cytoplasm. They can move from cell to cell. Insertion into a plasmid of a transposon carrying an antibiotic resistance gene provides a mechanism by which antibiotic resistance can be transferred from cell to cell.**



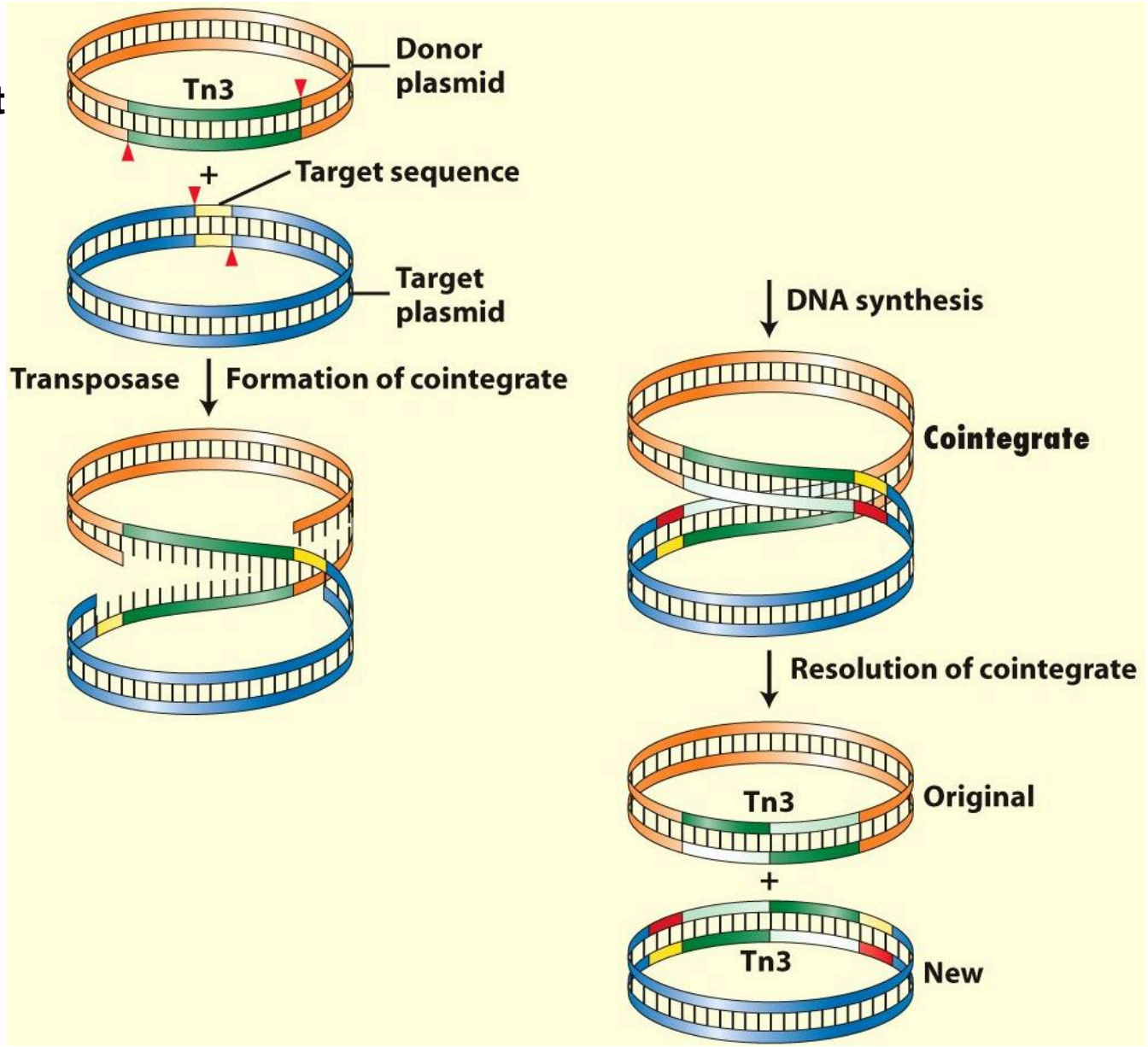
# Mechanism of Simple Transposition by IS10



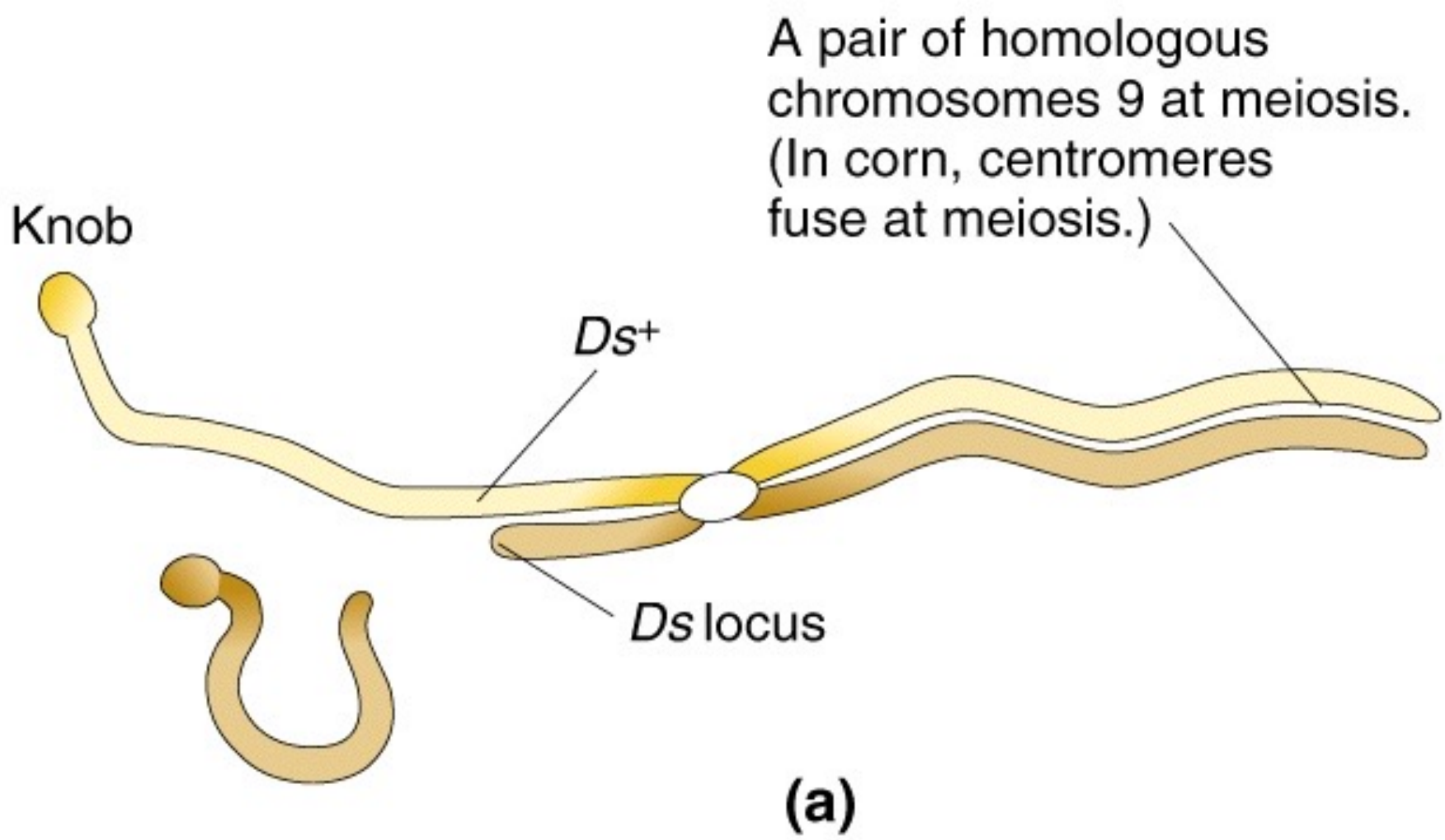
Schematic of the integration of an IS element into chromosomal DNA. As a result of the integration event, the target site becomes duplicated to produce direct target repeats. Thus, the integrated IS element is characterized by its inverted repeat (IR) sequences flanked by direct target site duplications. Integration involves making staggered cuts in the host target site. After insertion of the IS, the gaps that result are filled in with DNA polymerase and DNA ligase. (Note: The base sequences given for the IR are for illustration only and are not the actual sequences found, either in length or sequences.)



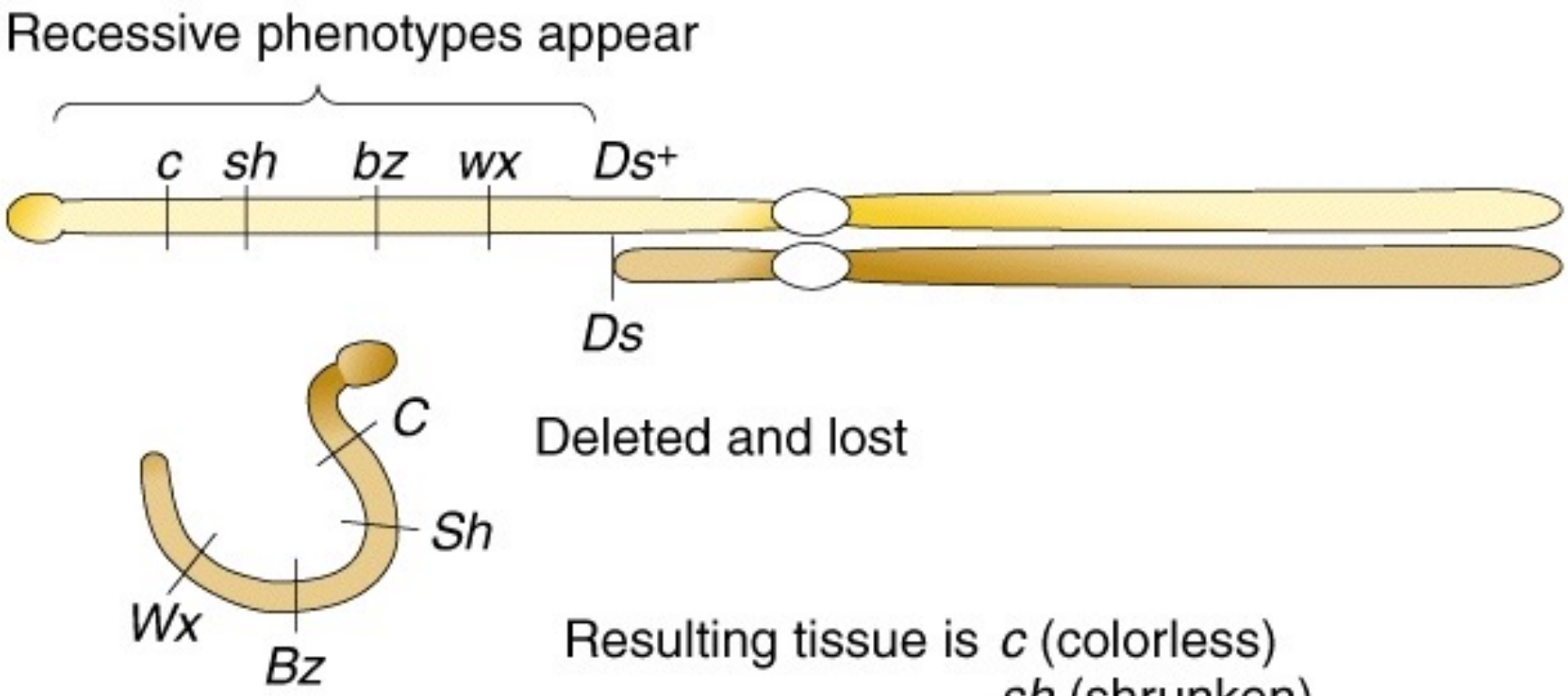
**Replicative transposition** involves the formation of a cointegrate. The initial event involves cleavage of donor and recipient strands at only two sites, followed by ligation and DNA synthesis.homologous recombination followed by resolution of the Holliday junction results in the formation of two molecules, both containing transposons. The new chromosomal insertion is flanked by direct repeats of the target sequence.



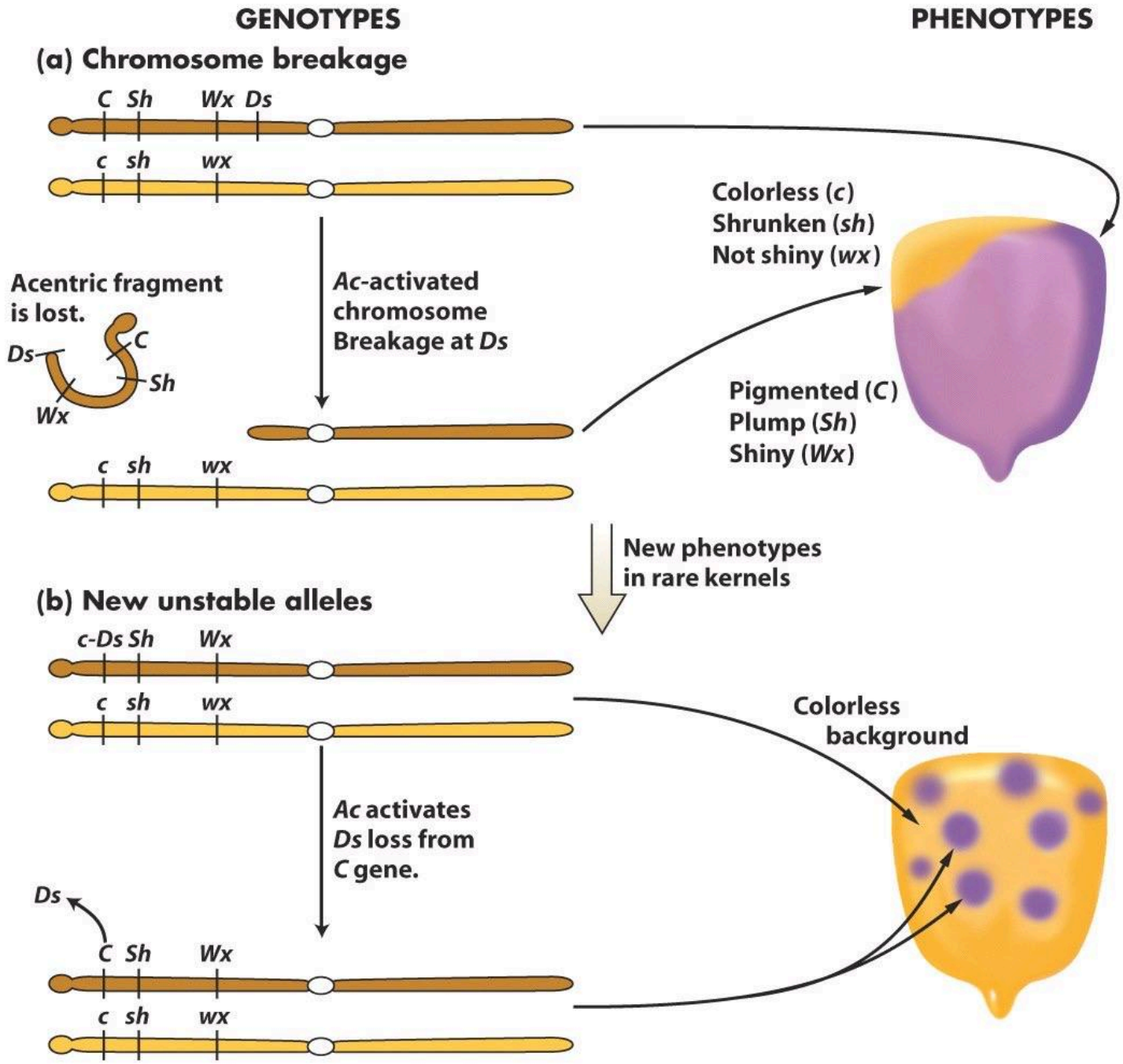
# Autonomous and non-autonomous transposons in corn

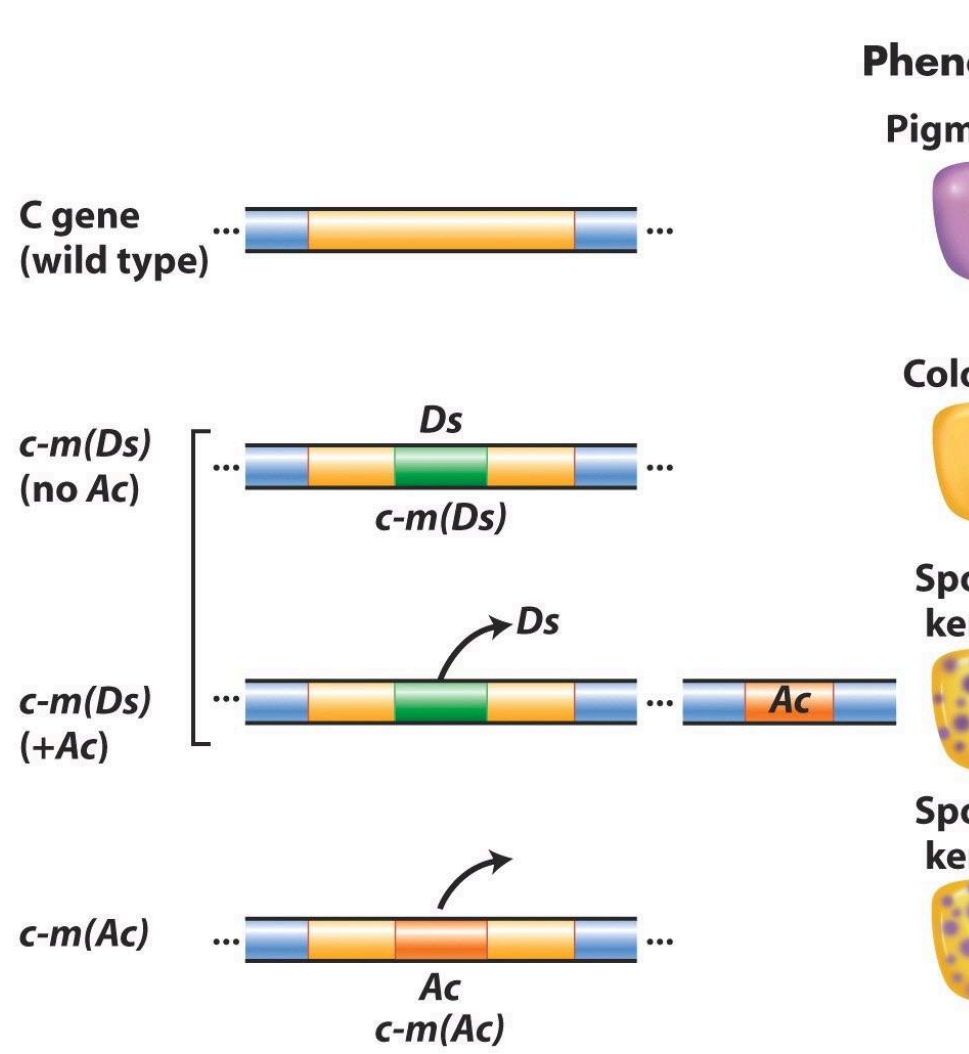


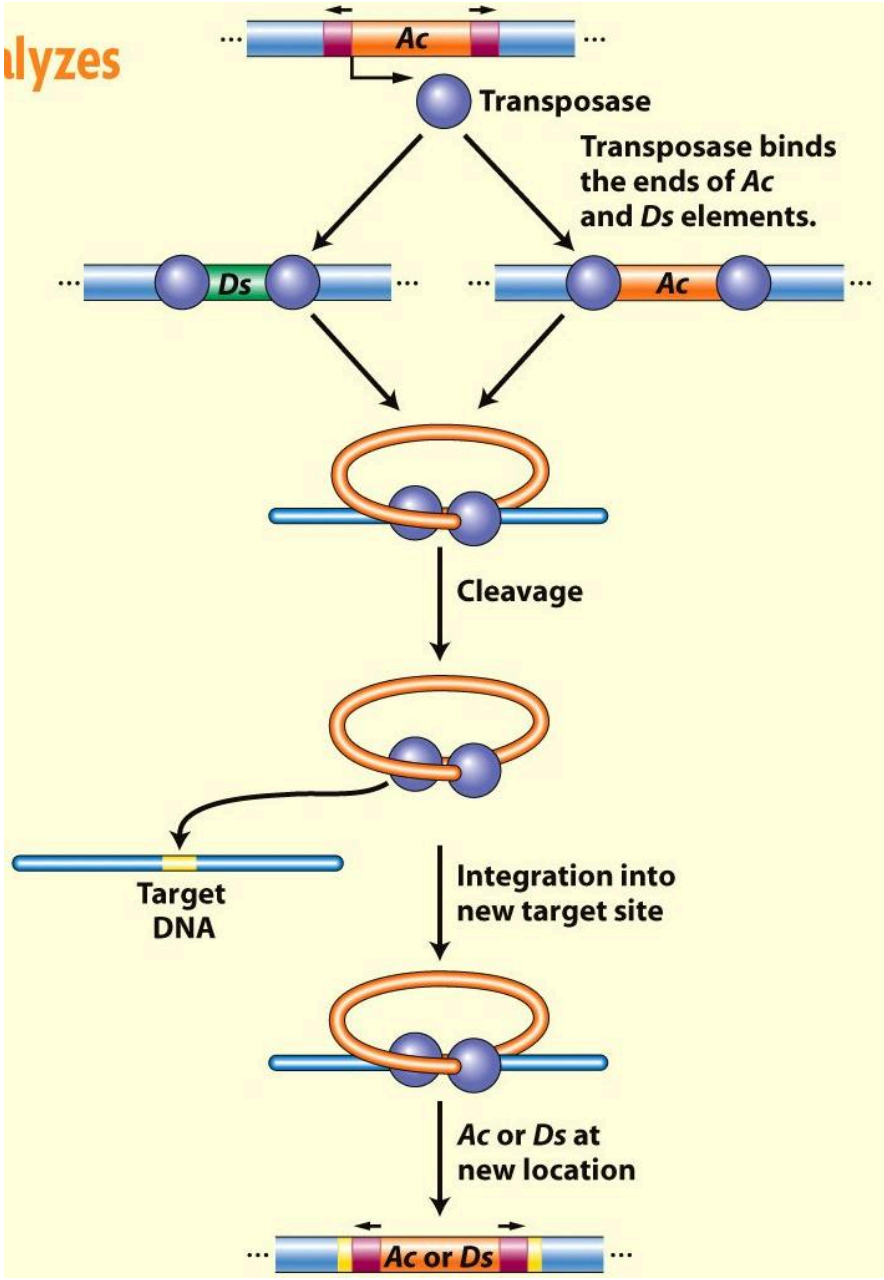
# A large chromosome fragment is sometimes lost in the presence of the Ds allele.




**(b)**


GENOTYPES
PHENOTYPES
(a) Chromosome breakage
C Sh Wx Ds
c sh wx
Colorless (c)
Shrunken (sh)
Not shiny (wx)
Acentric fragment
is lost.
Ds
C
Sh
Wx
Ac-activated
chromosome
Breakage at Ds
Pigmented (C)
Plump (Sh)
Shiny (Wx)
c sh wx
New phenotypes
in rare kernels
(b) New unstable alleles
c-Ds Sh Wx
c sh wx
Colorless
background
Ac activates
Ds loss from
C gene.
Ds
C Sh Wx
c sh wx




**Transposon art.** Mobile genetic elements caused these prized color patterns in morning glories.

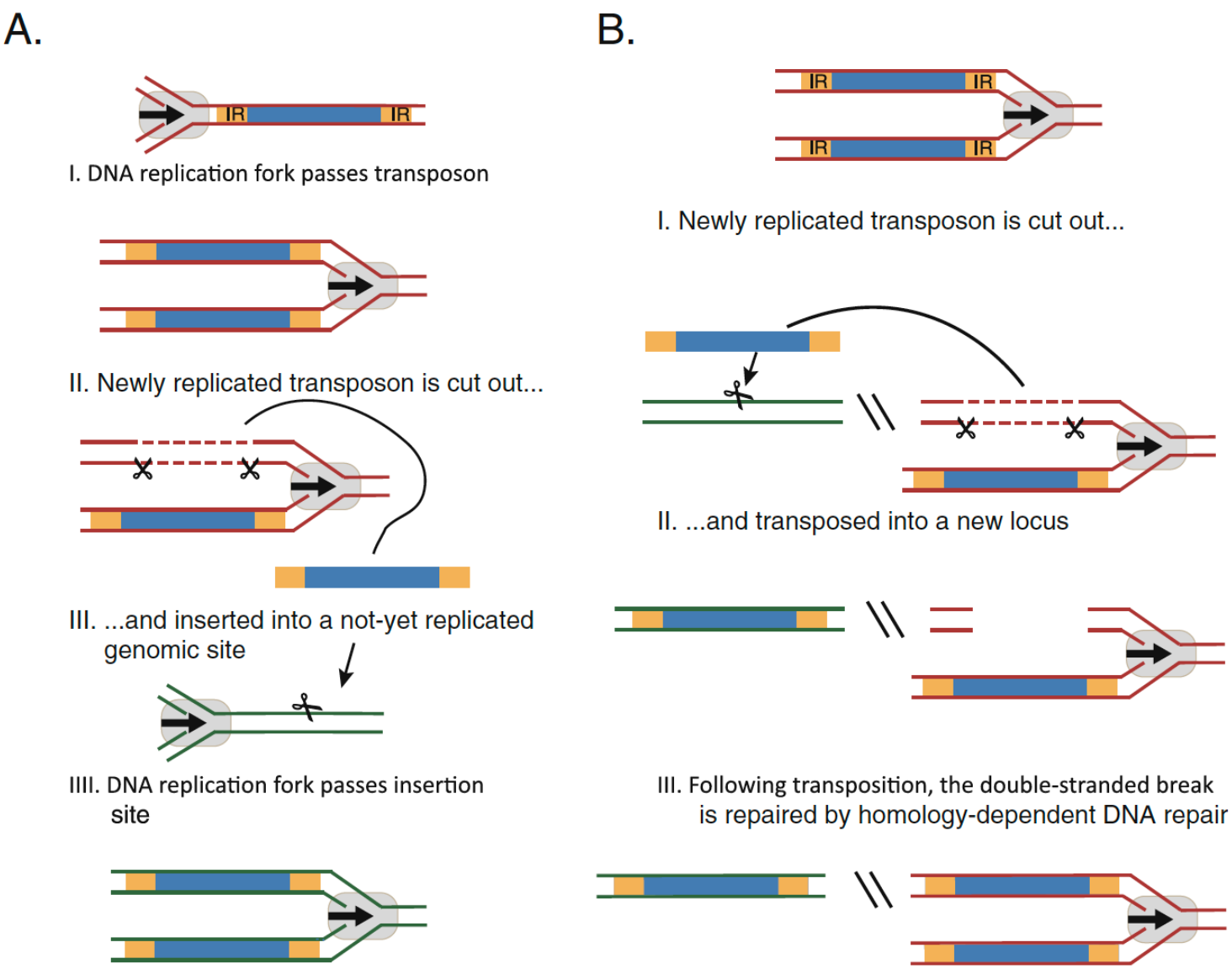



**Figure 3 Models of replicative transposition. (A)** After replication, the transposon is excised and integrated into a yet unreplicated genomic site thus duplicating the newly inserted transposon. **(B)** The double-stranded break created by transposition at newly replicated DNA is repaired using the sister chromatid as a template for homology-directed DNA repair, leading to reconstitution of the excised transposon. IR, terminal inverted repeat.

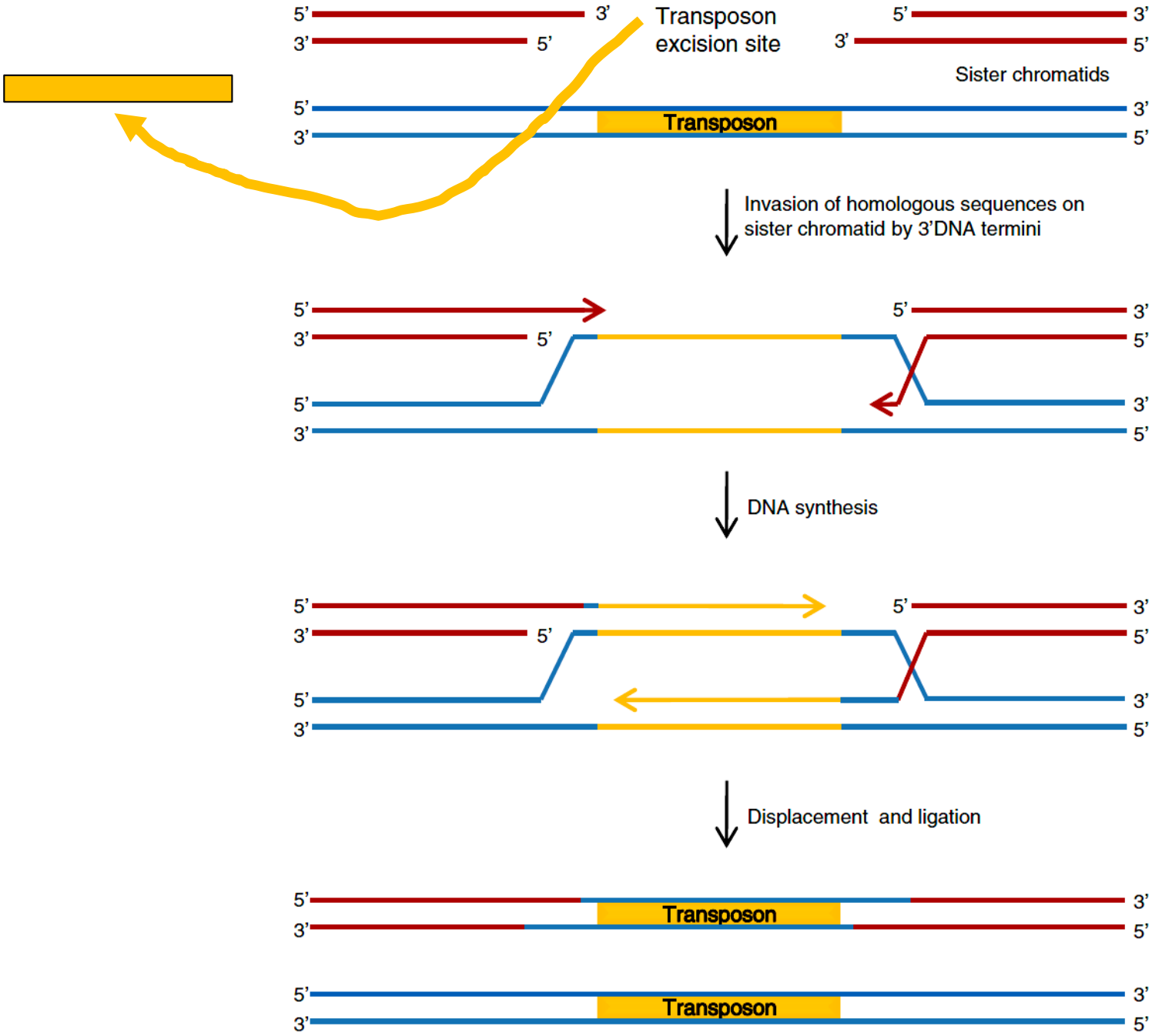
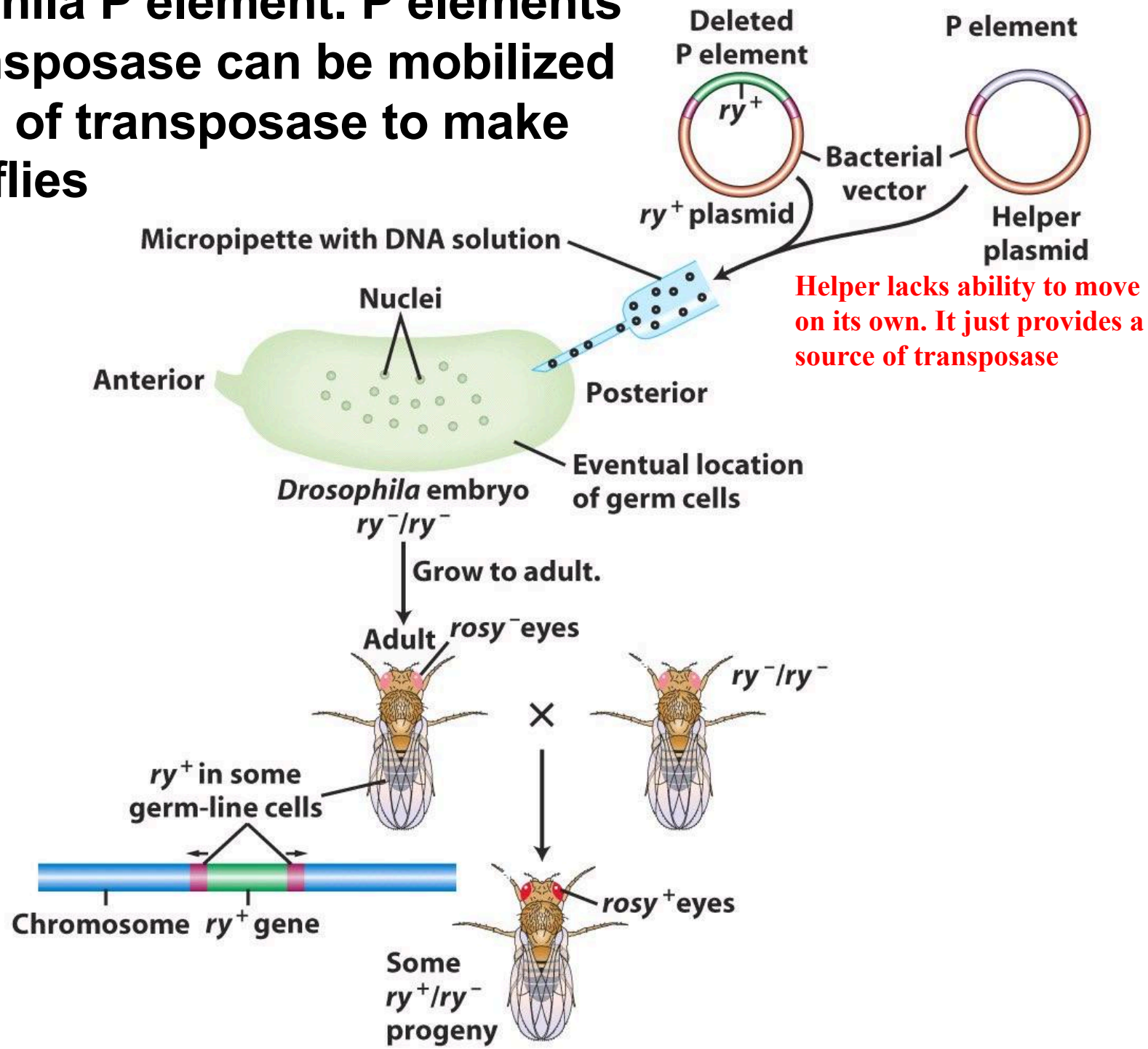



**Figure 4 Homology-dependent DNA repair by synthesis-dependent strand annealing (SDSA).** Following excision, the 3′-DNA termini from the double-stranded breaks invade the homologous sequence on the sister chromatid. The homologous sequence is then used as template for DNA synthesis and the final, elongated 3′-DNA termini anneal to each other and are joined with the 5′ ends by ligation.

# The Drosophila P element. P elements lacking transposase can be mobilized by a source of transposase to make transgenic flies

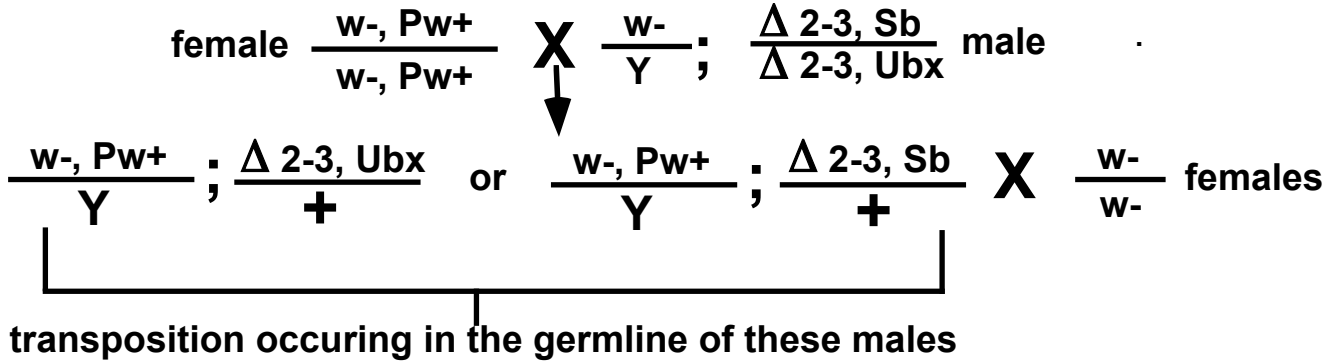



Helper lacks ability to move on its own. It just provides a source of transposase

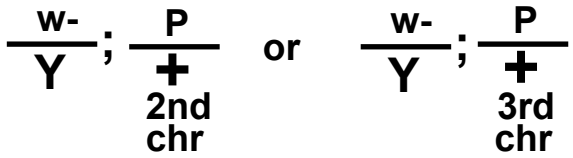
# Hopping a transposon in flies off the X chromosome, and onto an autosome.

**Pw+ = a transposon that carries a wildtype copy of the w gene on the X chromosome.**

**Δ 2-3, Ubx and Δ 2-3, Sb = these are third chromosomes that carry an immobilized source of transposase (Δ 2-3), as well as a dominant visible marker (Ubx or Sb). Transposase is normally only active in the germline. However, Δ 2-3 is active in somatic cells as well. This has the consequence that transposons are continually being mobilized in somatic tissues. If the P element contains a cell autonomous marker gene such as w+ (red pigment) this mobilization can be observed as eye color mosiacism.**




**The P element can hop into the + version of the second or third chromosome. If this occurs, and the meiotic product (the sperm) also carries a Y chromosome, then the progeny will be a red-eyed male. If no transposition occurs or the P hops into outer space then male progeny will have white eyes.**




**There are a number of other male progeny types that will also be genrated. Some of these will still have the Δ 2-3 source of transposase. Others will simply have no P element transposition onto one of the chromosomes present in the gamete. These will all lead to progeny that are w-**

**1. Any red eyed male resulting from the above crossmust have had a transposition event off the X chromosome and onto an autosome or onto the Y chromosome (happens rarely), since males get their X (which in this case is w-) from the female.**

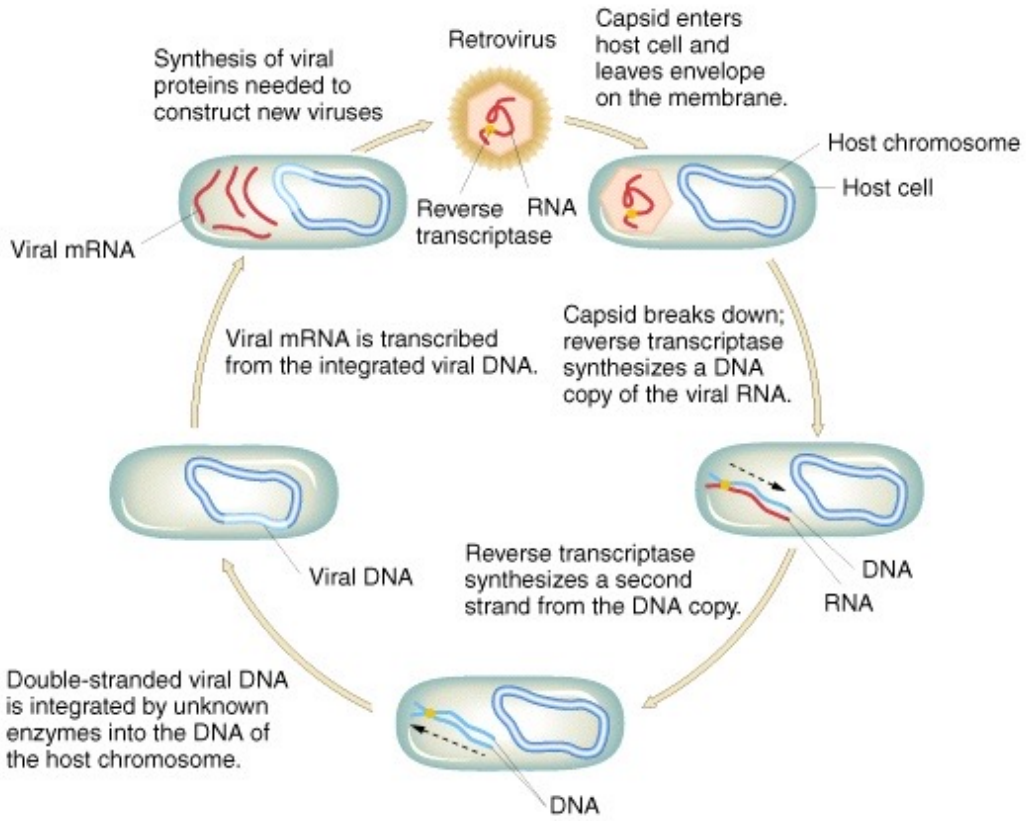
**2. Males that have both a P element and Δ 2-3 will have red and white variegated eyes as a result of somatic transposition of the Pw+ in somatic eye tissue.**

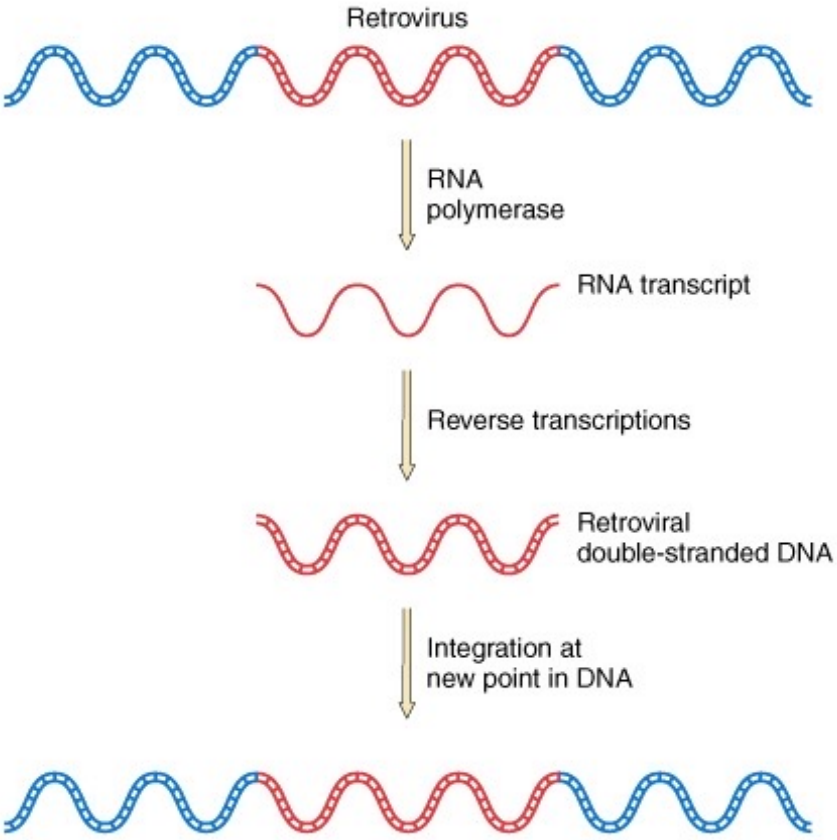
# The power of the P element

**In the early 20th century wild Drosophila melanogaster populations lacked the P element. We know this because people collected animals from throughout the world and kept them as stocks up through the present. They lack any P elements.**

**The P element entered D. melanogaster sometime in the 20th century, from another species. It is now ubiquitous (30+ copies) in ALL wild populations.**

**Retroviruses are RNA viruses that generate a double-stranded DNA intermediate using the enzyme reverse transcriptase. The double-stranded DNA intermediate can integrate into the genome, generating a provirus.**



# Retrovirus-like Retrotransposon

Yeast Ty1


**LTR: Long Terminal Repeat contains both promoter and poly-A sites**

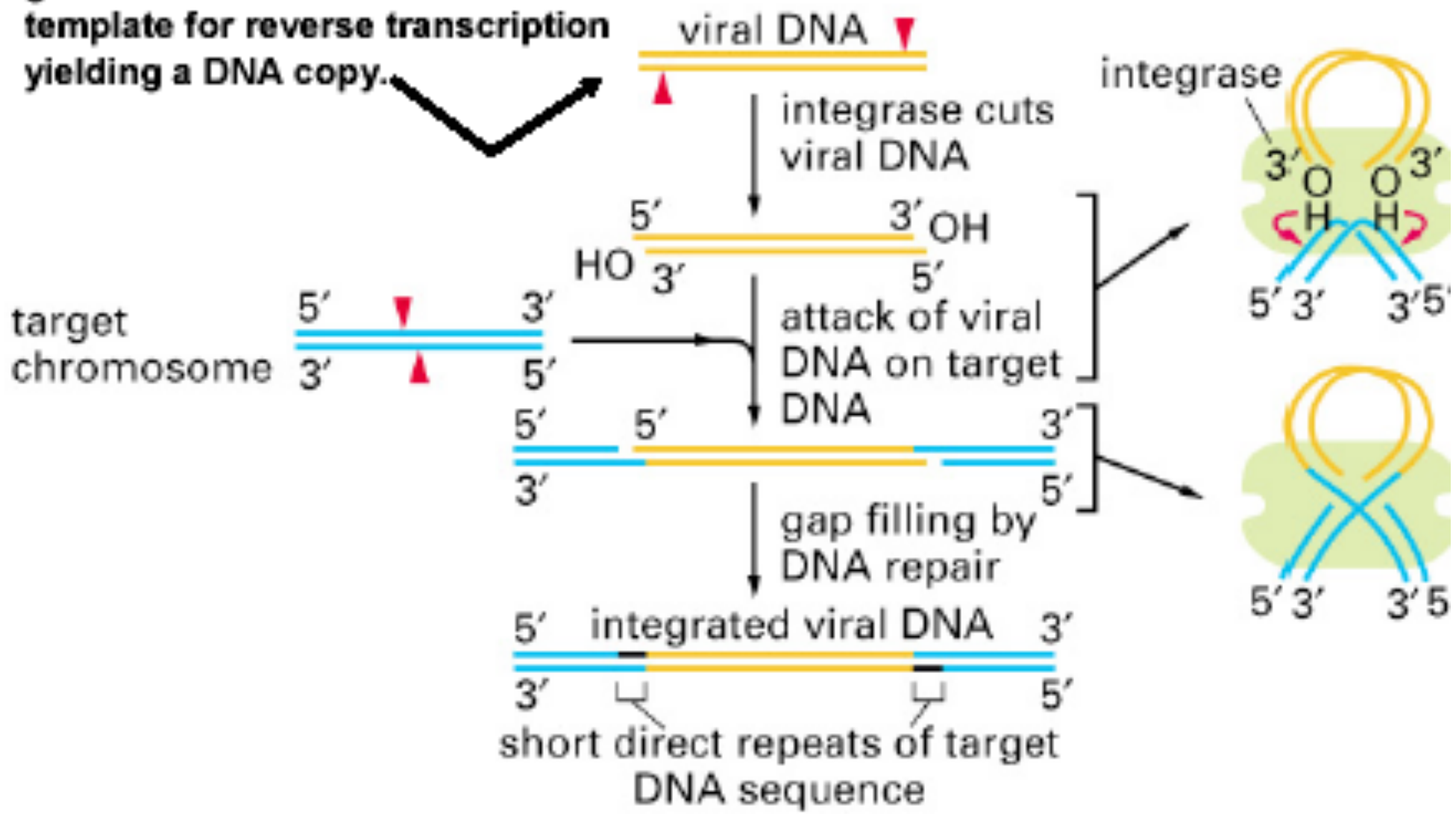
**TYA: encoding a polyprotein for the capsid (*gag*-like proteins)**

**TYB: encoding a polyprotein for enzymes used in transposition**

- ***pro*** **proteinase**
- ***int*** **integrase**
- ***rt*** **reverse transcriptase**
- ***rnh*** **RNaseH**

# Integrase Catalyzes Insertion of Retrotransposons

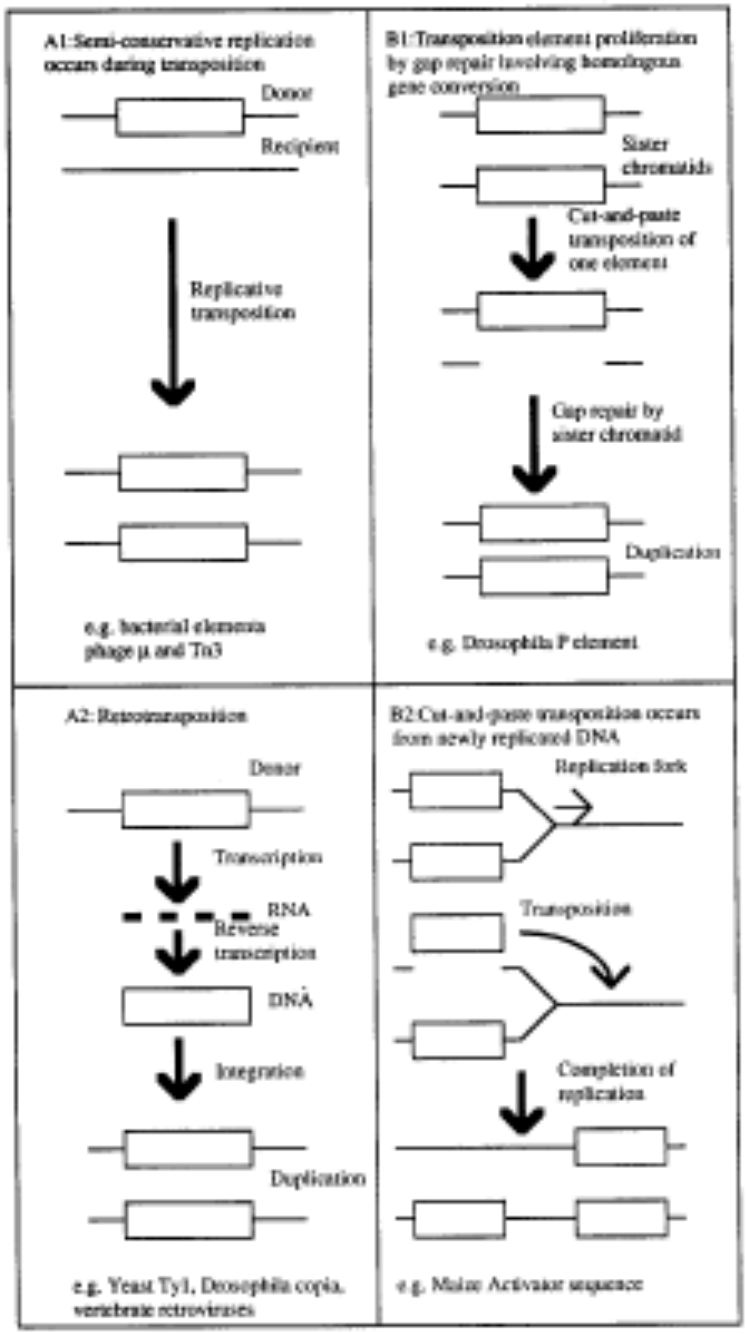
**Retrotranposon transcription generates RNA that serves as a template for reverse transcription yielding a DNA copy.**



## Mechanisms by which transposons and retrotransposons increase in copy number

**Replicative transposition**

**RNA synthesis followed by reverse transcription**



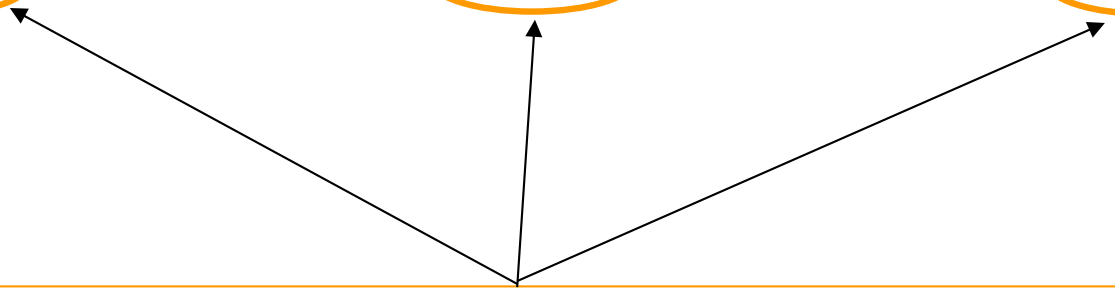

**Repair of a DNA Double-stranded break**

**Movement in front of a replication fork**

Fig. 1 Four ways in which transposition can lead to an increase in transposable element copy number. For

# Number and nature of interspersed repeats in human, fly and worm

| | Human | | Fly | | Worm | |
|---|---|---|---|---|---|---|
| | Percentage of bases | Approximate number of families | Percentage of bases | Approximate number of families | Percentage of bases | Approximate number of families |
| LINE/SINE | 33.40% | 6 | 0.70% | 20 | 0.40% | 10 |
| LTR | 8.10% | 100 | 1.50% | 50 | 0.00% | 4 |
| DNA | 2.80% | 60 | 0.70% | 20 | 5.30% | 80 |
| Total | 44.40% | 170 | 3.10% | 90 | 6.50% | 90 |



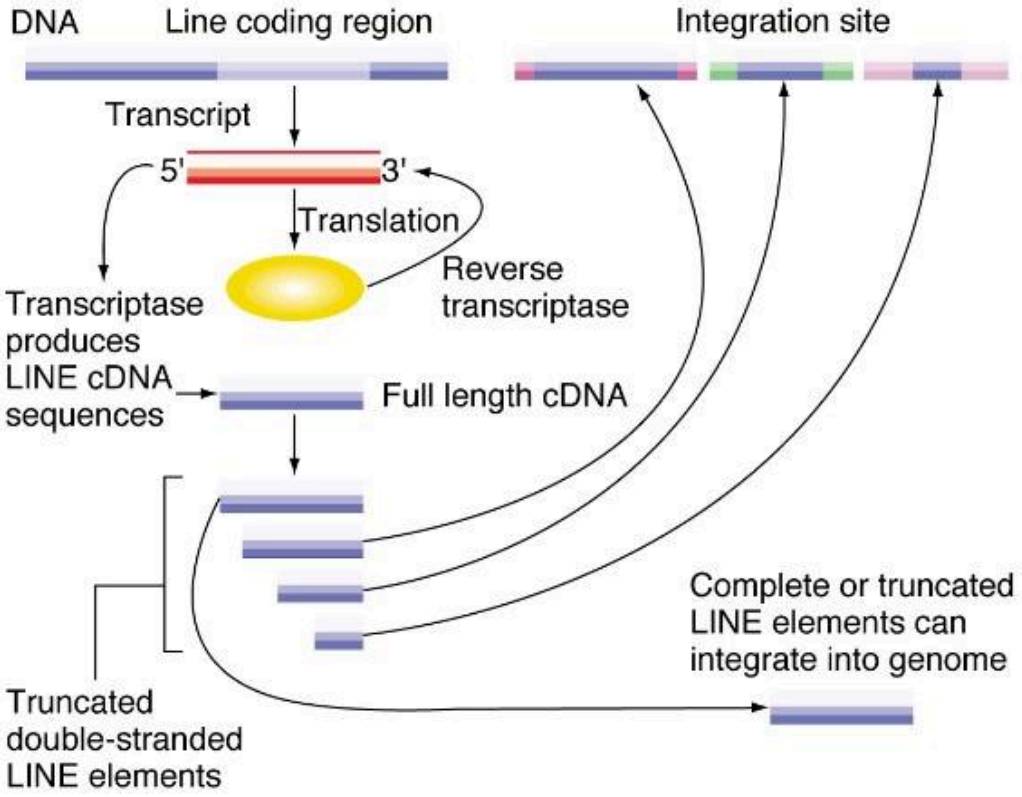
The euchromatic portion of the human genome has a much higher density of transposable element copies than fly and worm

# Transposons and genome structure

**Drosophila melanogaster: 90 different elements = 3% of genome**
**Mammals: LINES and SINES = 34% of genome**



**LINES are retroposons that derive from a "selfish" DNA sequence that encodes reverse transcriptase. A complete LINE sequence can be copied into RNA. Reverse transcriptase makes cDNA copies from the RNA. These copies may be complete or truncated. Both may then integrate into other sites in the Genome.**

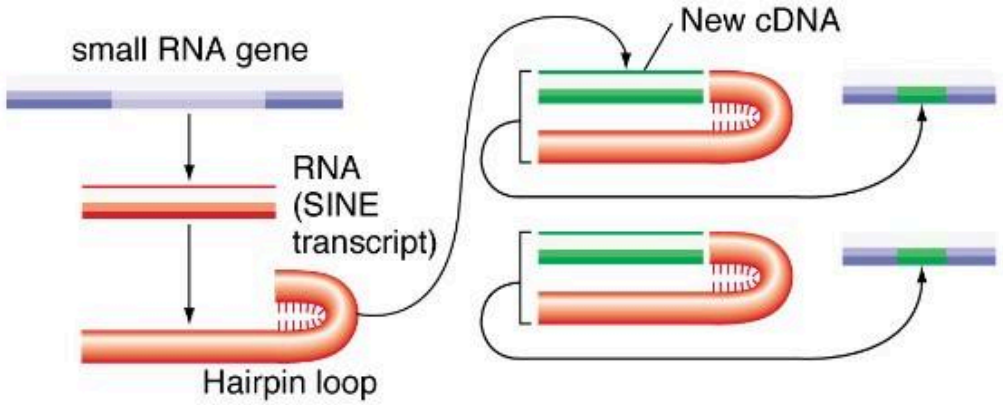



**SINES replicate through an RNA intermediate, but do not encode reverse transcriptase themselves. Instead They utilize reverse transcriptase present in the cell.**

**The Alu family of repetitive elements in the human Genome is an example of a SINE family. There are Than 500,000 Alu elements/ genome at 300bp/element.**

**The SINE element has evolved from normal cellular RNAs, most often tRNAs, but also an RNA that forms A component of the signal recognition particle, which Is required for protein translocation across the Endoplasmic reticulum membrane.**

**The important modification of these cellular RNAs that Has occurred are modifications in the 3' end of the Transcript that lead to self complementarity. This Provides a binding structure for reverse transcriptase.**



# How a Quarter of Cow DNA Came From Reptiles

By hopping between species, jumping genes have radically altered the course of animal evolution.

By Ed Yong

# Transposon mobilization: Consequences for genome evolution over time

1. Inversions as a result of recombination between inverted repeats.

2. Deletions as a result of recombination between direct repeats.

3. Unequal crossing over between repeats (regions of micro-homology) leads to translocations, deletions, and gene duplications.

4. Gene inactivation as a result of transposon insertion.

5. Gene activation as a result of a transposon (or retrovirus) inserting near a gene, and driving the transcription of that gene from a transposon promoter.

6. Once transposons enter the germline of a species they can multiply and become ubiquituous very rapidly.

   Drosophila P elements. World-wide spread within 30 years

   Alu sequences in primates and humans.

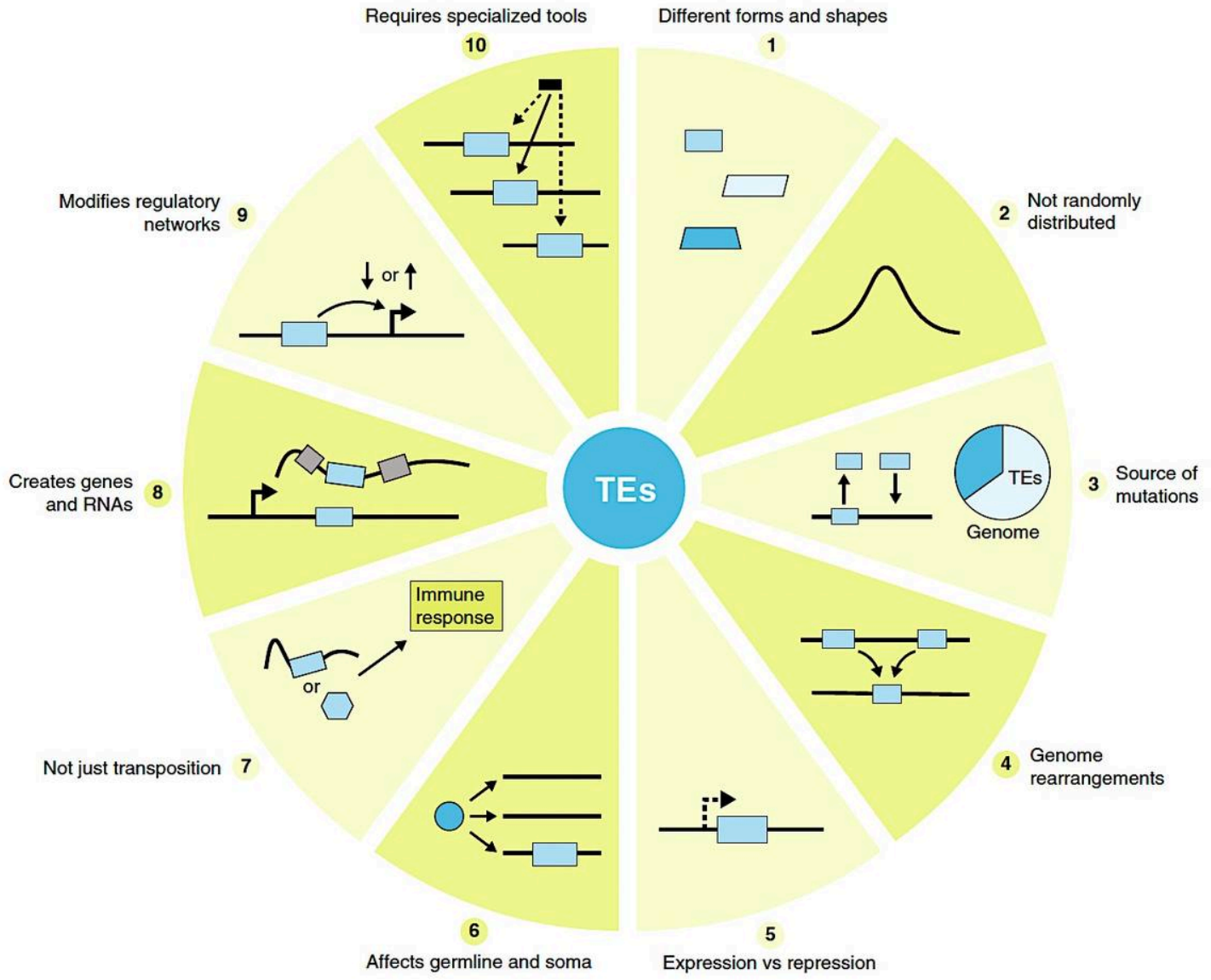



**Fig. 2** Ten things you should know about transposable elements (TEs). Examples of how TEs can impact genomes in direct and indirect ways. Blue boxes represent TEs, gray boxes represent canonical exons, and the black box represents a sequencing read. Right-angled arrows represent gene or TE promoters