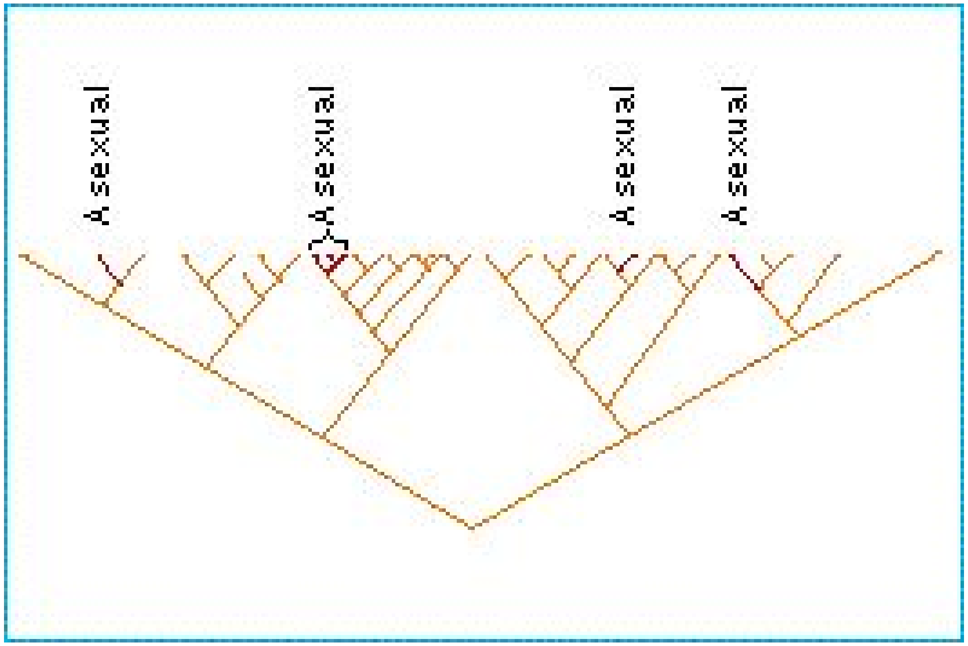
Roadmap

- Sexual Selection
- Evolution of Multi-Gene Families
  - Gene Duplication
  - Divergence
  - Concerted Evolution
  - Survey of Gene Families

One minute responses

- Q: How do aphids start producing males in the fall?
- A: "Asexual females sense the changing photoperiod and temperature and respond by parthenogenetically producing sexual females and males. Males are produced genetically by the loss of one X chromosome during parthenogenetic oocyte division and can be winged or unwinged. Since only sperm containing an X chromosome are viable, sexual females lay only female eggs on the host plant." Srinivasan and Brisson 2012
- Q: Was the X^* chromosome in mice produced due to human intervention?
- A: No. It apparently arose multiple times in genus $Akodon$ before humans came to South America.

Evidence for long-term problems with asexuality



Asexual species appear evolutionarily short-lived (bdelloids are the one huge exception)

How is sexual reproduction maintained?

- One of the most debated points in evolutionary biology
- Human need for tidy answers may be a problem
- Perhaps multiple theories are partially correct under different circumstances
- A kind of species "genetic drift" may also be involved:
  - Sub-optimal species may persist by chance
  - If they have better long-term prospects, eventually species of their type will predominate

Sexual selection

- Start from:
  - Females like bright feathers on a male as they show health
  - Males evolve to have bright feathers to attract females
- Over time:
  - Males with more extreme feathers attract more females
  - Females who choose extreme males have more attractive sons
- This is a feedback loop

Was this a good idea?

- This male has high sexual fitness, but what about his overall fitness?
  - Every mating requires a male
  - If many males die, the few survivors sire a lot of offspring
  - Sexual selection can directly oppose fitness selection

Image by Jatin Sindhu

An anomaly: Spotted Sandpiper

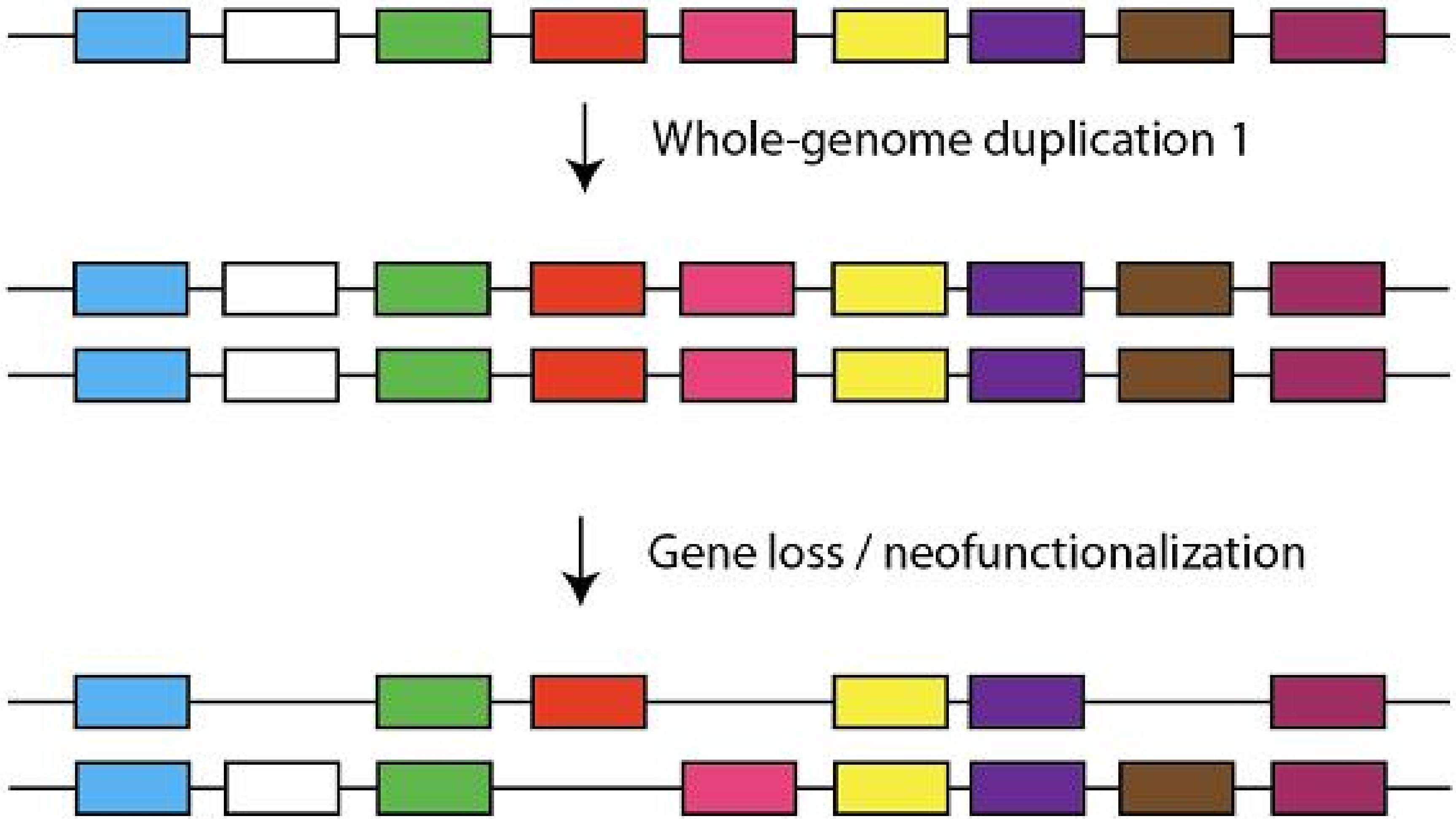
- Females can lay multiple clutches per breeding season
- Females compete (and fight!) for males, and the males raise one clutch each
- This may have evolved when:
  - Sandpipers nested in the Arctic and had to produce clutches very fast
  - Spotted Sandpipers moved to the temperate zone
  - Now females could produce multiple clutches–but not raise them
- This is a dramatic reversal of the usual pattern in birds

Image by Mdf

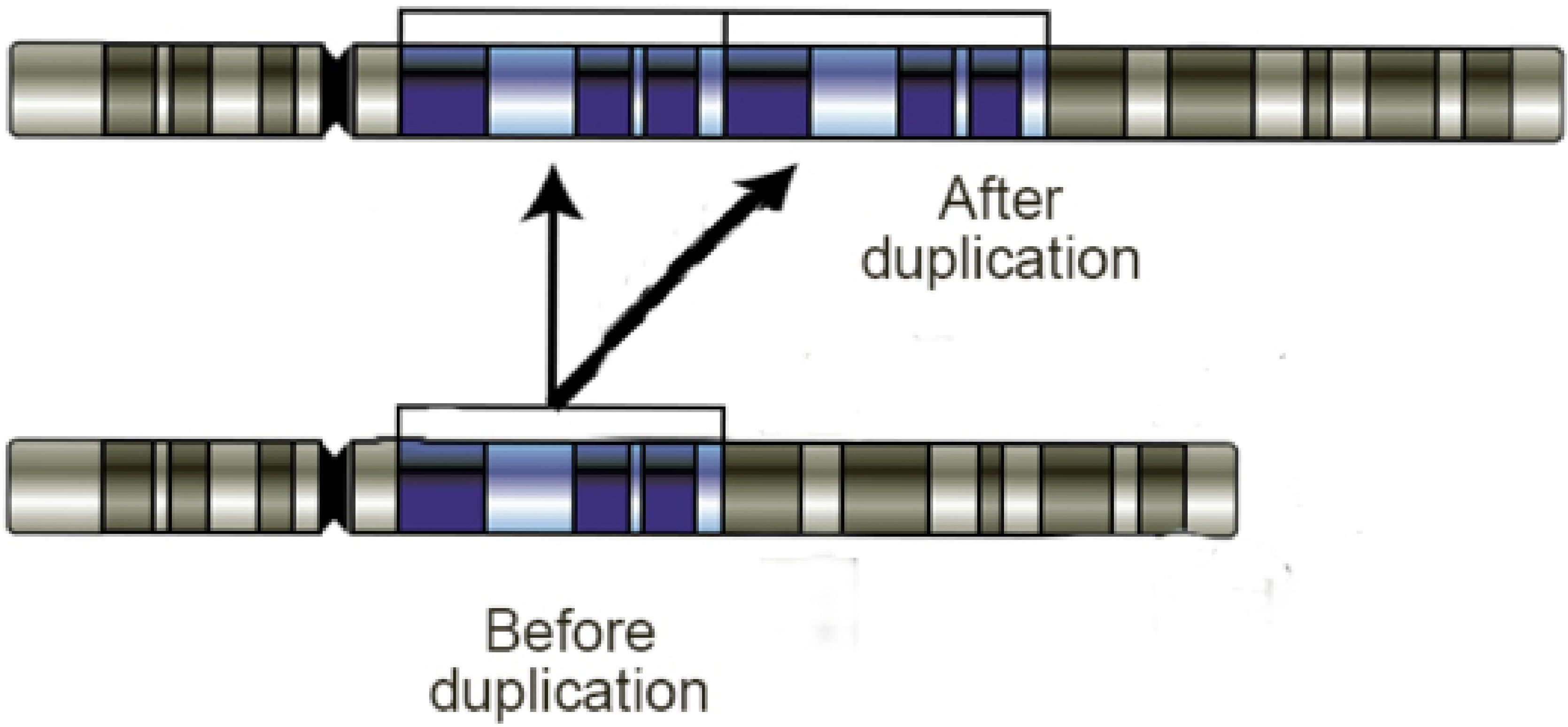
New Genes and Gene Families

- Where do novel genes come from?
- Why do genes occur in multi-gene families?
- What are the evolutionary consequences of duplicated genes?

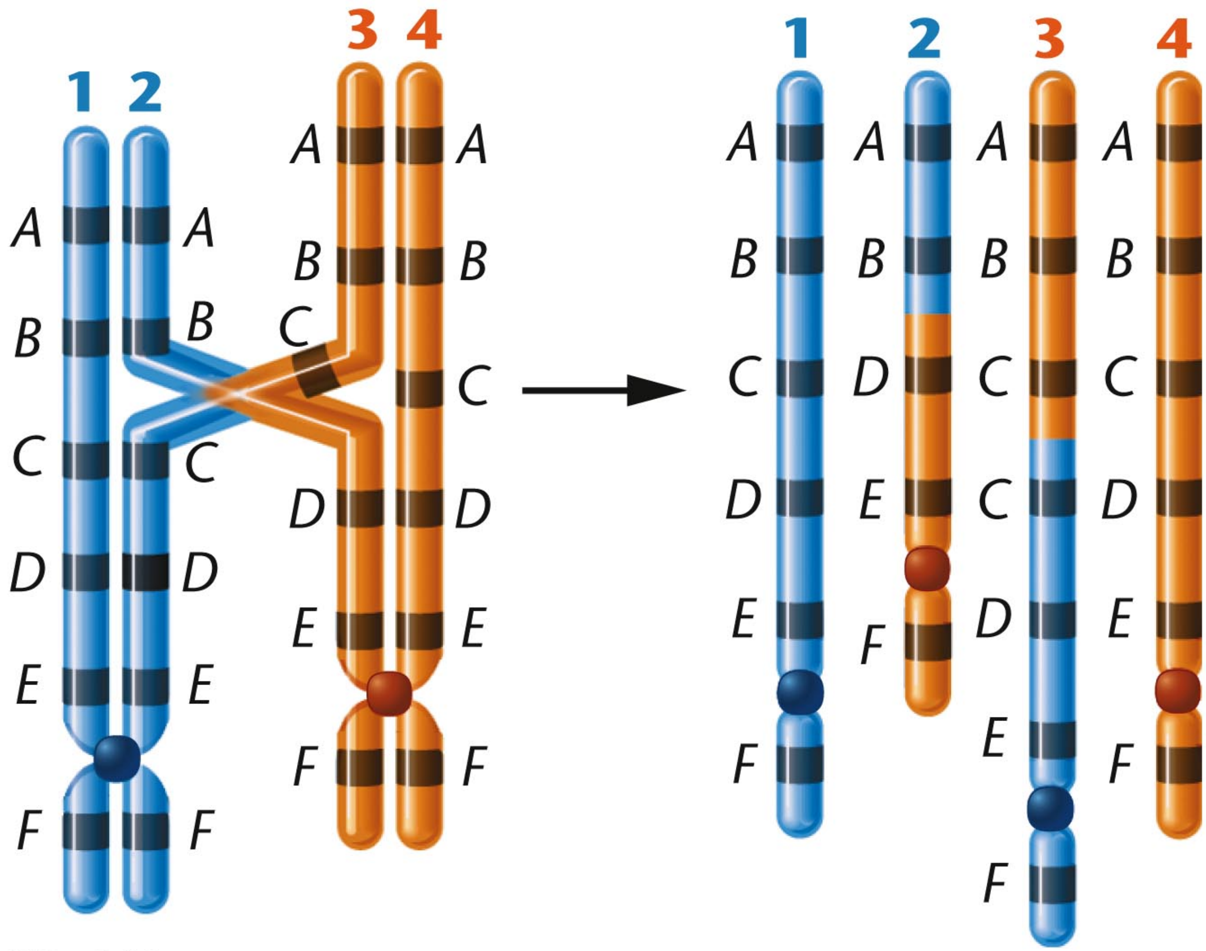
Genome doubling



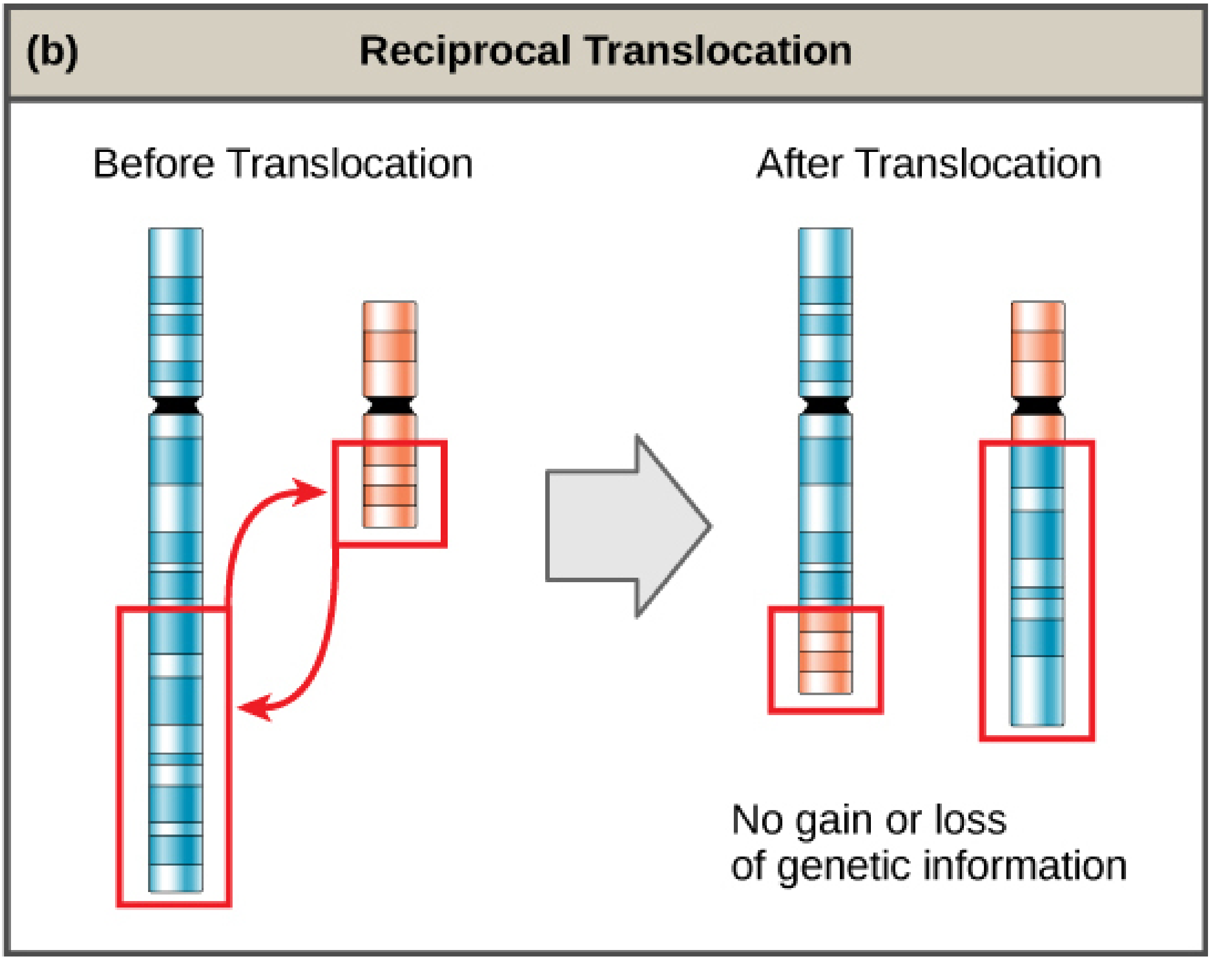
Local duplication



Unequal crossing over



Translocation

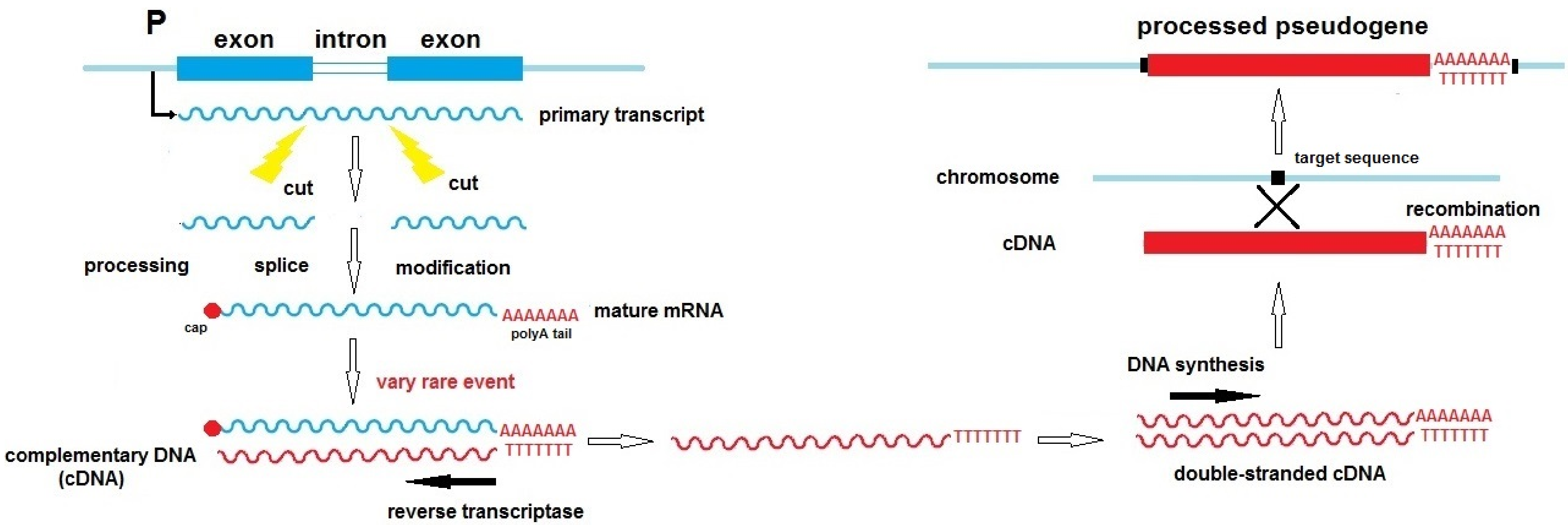


Discussion

Unequal crossing over and translocation don't change the number of gene copies (they just move them around)

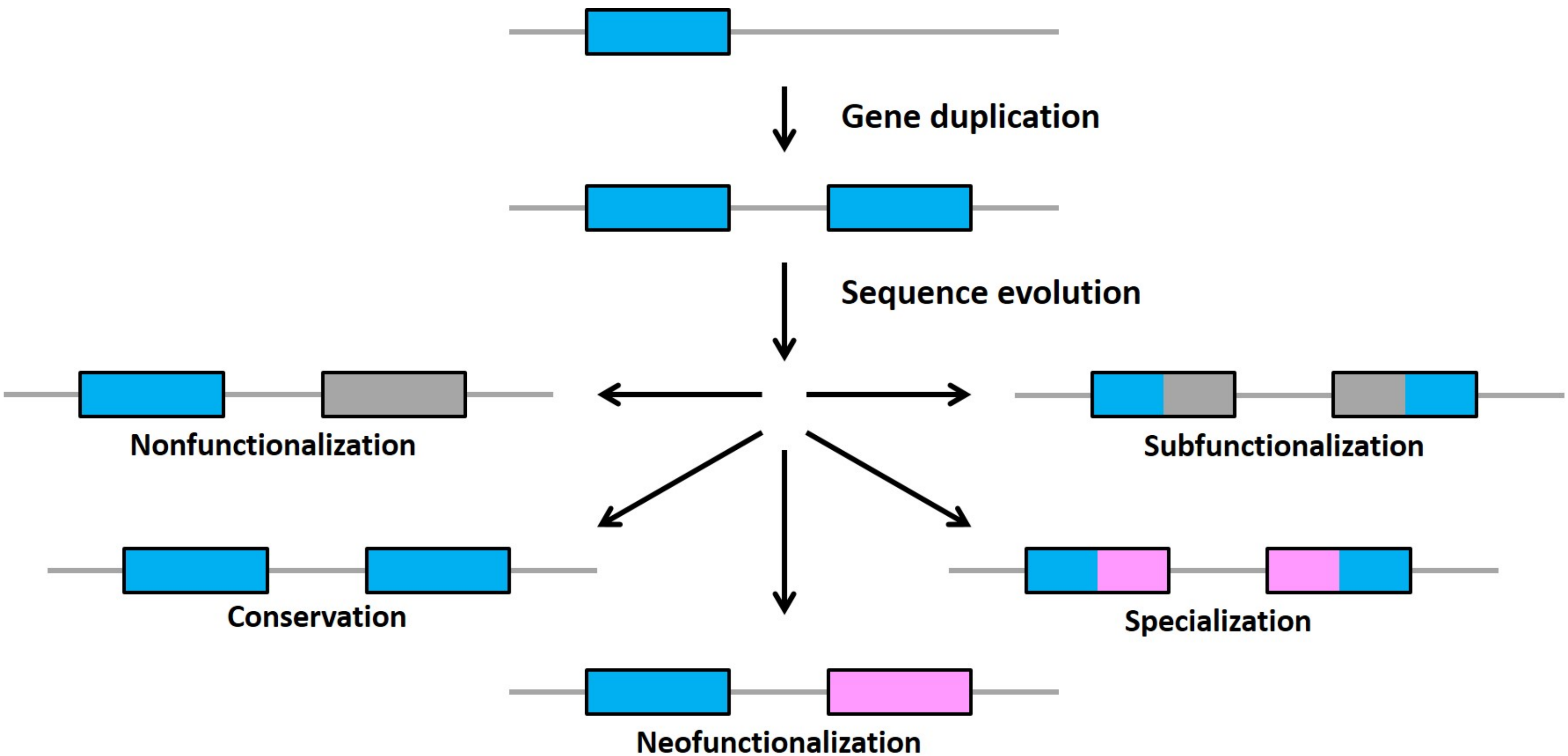
Why are they described as pathways to gene duplication?

Processed pseudogenes



These are usually not functional, but could be raw material for building a functional gene.

Possible fates of a duplication



Red-Green Color Vision–Splitting the Old Function

The red-vision and green-vision genes of humans are extremely similar and are believed to be a gene duplication. However, they have specialized on slightly different wavelengths, giving humans more complete color vision than we could have with only one gene.

```
----------- Gene ----------- Gene -----------
```

Red-Green Color Vision–Splitting the Old Function

This particular gene family is unstable, because R and G are next to each other. It is easy for a faulty recombination to produce chromosomes with an R/G hybrid gene.

```
-------   Gene   -------   Gene   -------
                 -------   Gene   -------   Gene   -------
```

A crossover can produce either of:

```
-------   Ge ne   -------
-------   Gene    -------   Ge ne   -------   Gene   -------
```

Since R and G are on the X chromosome, male humans are hemizygous for them. This explains the high frequency of R/G colorblindness in men.

HLA examples

A duplication followed by gene deterioration:

- HLA-AR locus: apparent duplication of HLA-A
  - Shows signs of past selection
  - High variability in antigen-binding region
  - Multiple stop codons and other harmful-looking mutations
  - Apparently produces no protein

- It was probably functional for a while, but now it's dead

HLA examples

Duplications followed by gene specialization:

- HLA-A, -B, and -C
  - Shows signs of past selection
  - High variability in antigen-binding region
  - Clean sequences without stop codons
  - Different expression levels in different tissues
  - Associated with resistance to different diseases

- HLA-C is less strongly expressed and associated with few diseases; it may be on the borderline between useful and redundant

Gene Duplication–Discussion

What determines whether a duplicated gene will deteriorate or take on a new function?

Gene Duplication

Advantages of gene duplication:

- Evolve a new function without losing the old one
- Fine-tune a gene for two different tasks
- Allow everyone to have both alleles of an overdominant system

Gene Duplication

In some primates, there is only one locus for red/green color vision, and red and green are alleles. A female can have human-like color vision:

```
-----  Gene  -----
-----  Gene  -----
```

but many females are colorblind homozygotes, and all males are colorblind.

Practice question: what are the optimal allele frequencies to maximize color-vision females?

Gene Duplication resolves overdominance

- Two-gene color vision:
  - (Almost) everyone has color vision
  - All individuals equally capable
- One-gene color vision (on X):
  - Half of females and all males color-blind
  - Color-blind individuals are a mix of red-sensitive and green-sensitive
- Could this ever be good?
  - Color-blind individuals excel at spotting camouflaged things
  - Color-vision individuals excel at spotting colored things
  - Division of labor in a social animal?

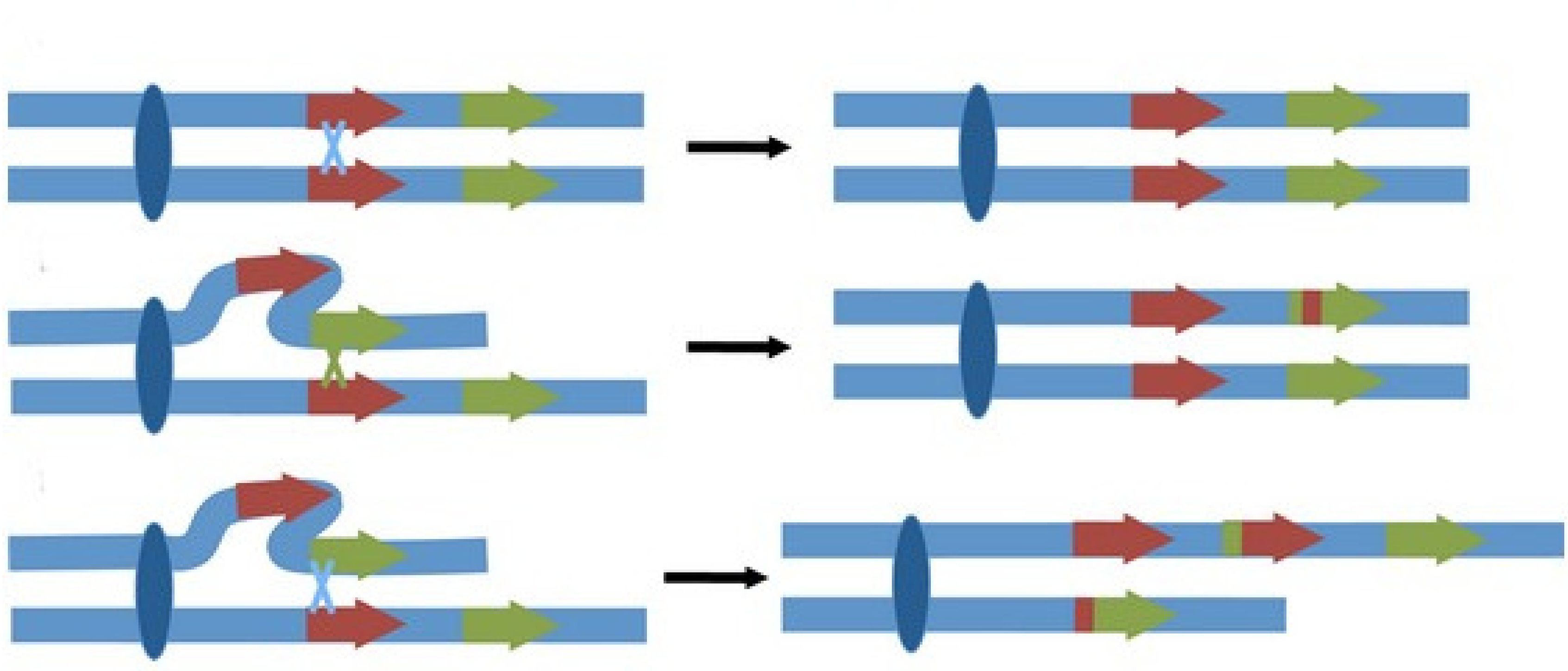
Concerted Evolution

Fates of duplicated genes:

- Divergence to fulfill new functions
- Deterioration and loss
- Concerted evolution–all copies remain highly similar

Concerted evolution is most common when the genes are clustered together on a chromosome, often as a **tandem array** or long series of head-to-tail gene copies.

What can make copies similar?



Green X: gene conversion
Blue X: crossing over

Concerted Evolution

- Concerted evolution more likely when:
  - repeats are tandem (adjacent)
  - number of copies is large
  - selection favors making lots of protein (rRNA genes)

- Concerted evolution less likely when:
  - repeats are scattered
  - number of copies is small
  - no selective advantage to "redundant" copies

Concerted Evolution

- Human R/G genes are on the borderline between concerted evolution and divergent evolution

- Forces that push convergence:
  - Genes are close together
  - Sequences are very similar

- Forces that resist convergence:
  - Full color vision is useful
  - X-linkage means that bad chromosomes are more exposed to selection

- If R and G were on different chromosomes, color blindness would probably be much less common

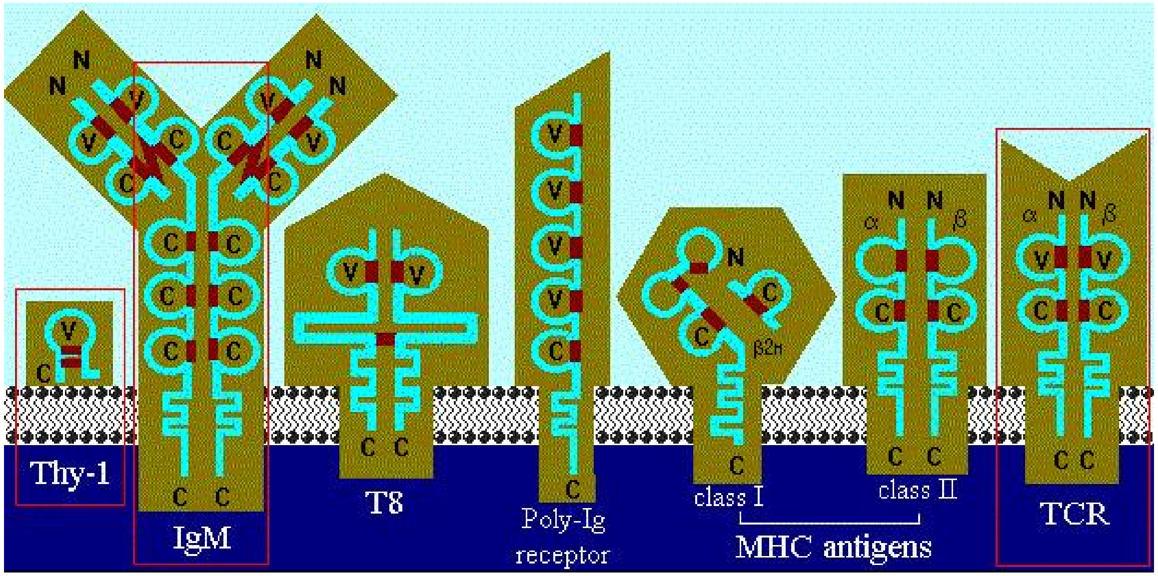
Multi-gene Families

Most genomes are full of multi-gene families of all sizes, from two up to thousands or more.

Some notable human examples:

- Alu transposable elements, tens of thousands of copies.
- HLA loci, around a dozen
- Antibody variable-region loci, dozens to hundreds
- R/G color vision loci, two or three

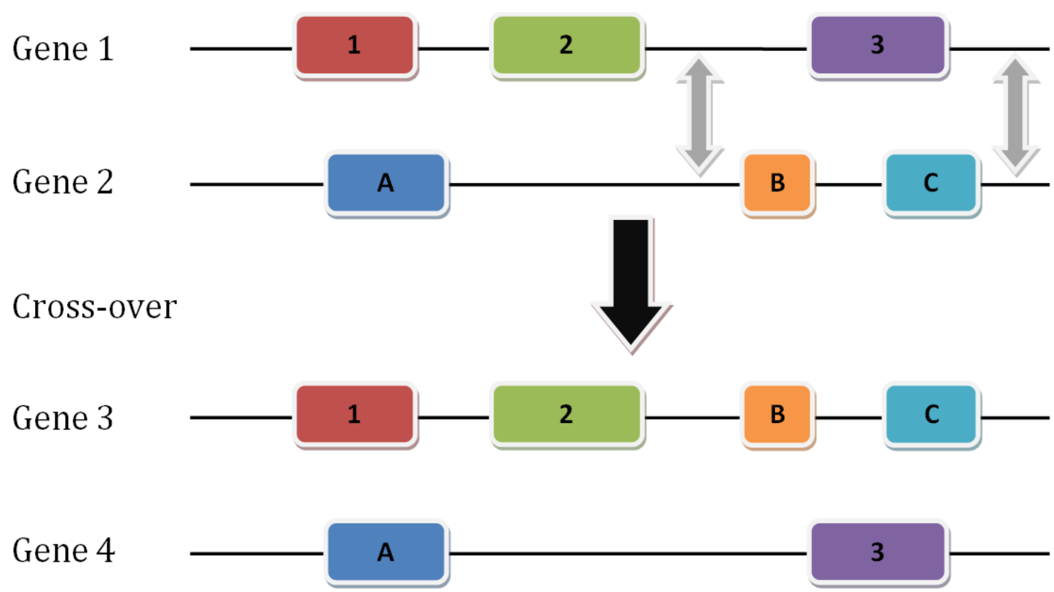
Multi-gene Families



We can also recognize "superfamilies", families of families, such as the immunoglobulin genes. They all share part of their structure, but other parts appear unrelated.

Exon shuffling

- New functions can arise by combining parts of old genes
- This is easier if exons represent functional units
- Could this be selected for? (Awfully long term selection!)
- Even if it's not selected it could be useful



One-minute responses

- Tear off a half-sheet of paper
- Write one line about the lecture:
  - Was anything unclear?
  - Did anything work particularly well?
  - What could be better?
- Leave at the back on your way out