PLANT OF THE DAY!

Yacón (*Smallanthus sonchifolius*) - relative of sunflower.

Grown in Andes for its crisp, sweet-tasting tuberous roots.

Roots contain inulin, an indigestible sugar, which means that although they have a sweet flavour, the roots contain fewer calories than would be expected.

Karyotypic changes and speciation

Chromosomal speciation

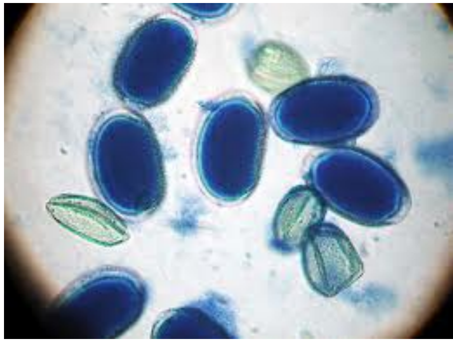
Big Questions

- Are chromosomal rearrangements important in speciation?
- How do chromosomal rearrangements become established in natural populations?

Chromosomal Speciation

- Caused by chromosomal rearrangements
- Fixed differences between species
  - > 95% of plant and animal species differ in their karyotype White (1978)
- How does this cause reproductive isolation?
  - Reduced fertility in hybrids
  - Reduction in recombination

(reproductive isolation/speciation about reducing interspecific recombination)



Inviable pollen due to rearrangements

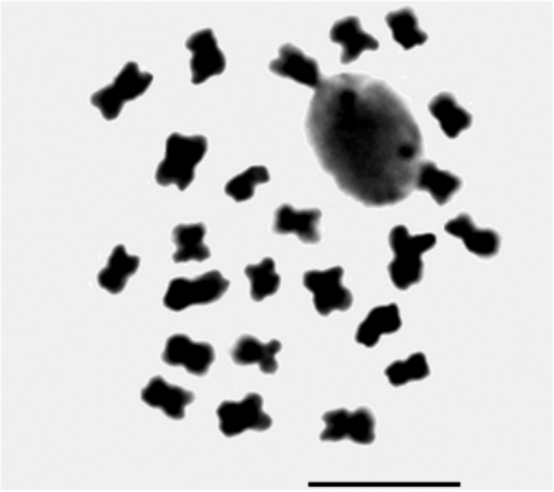


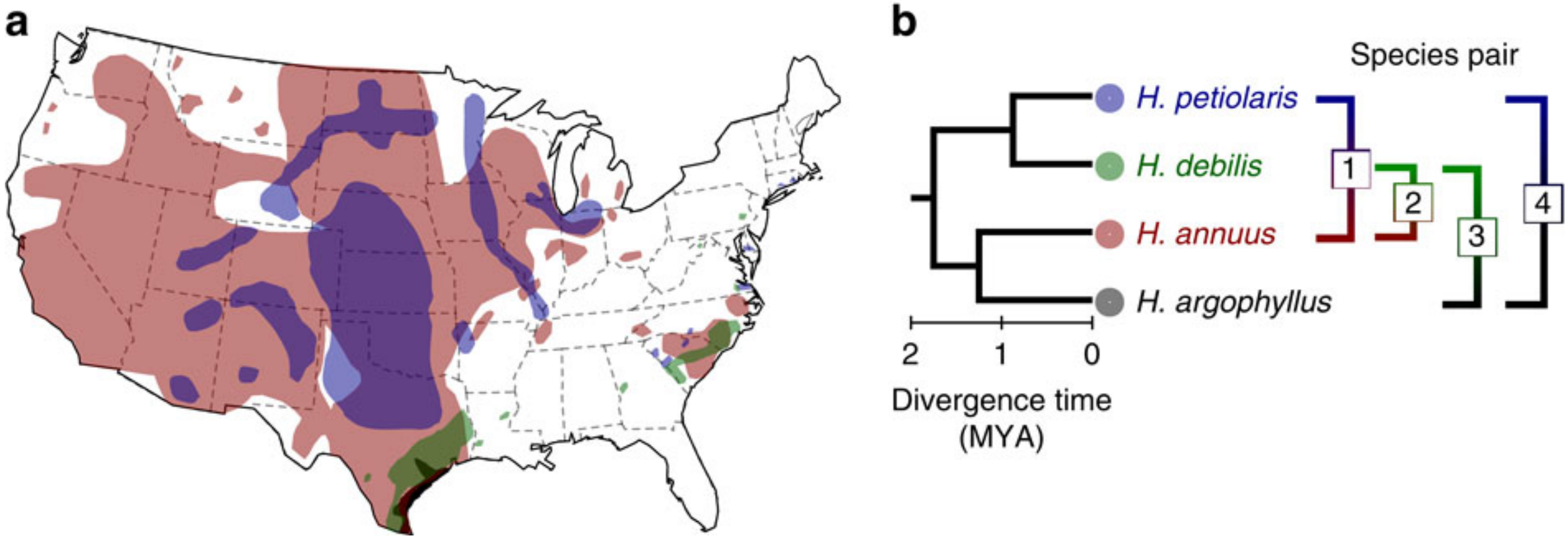
Figure 2 - Metaphase chromosomes (2n = 24) obtained from rosewood root tip cells pre-treated with 5 mM the herbicide oryzalin and Giemsa stained. The nucleolar organizing region can be seen in the short arm of the chromosome pair with secondary constrictions and satellites associated with the nucleolus. Note that after oryzalin treatment the chromosomes are condensed as in standard C-metaphase morphology and the nucleolus remains attached to the secondary constriction. Bar = 5 μm.

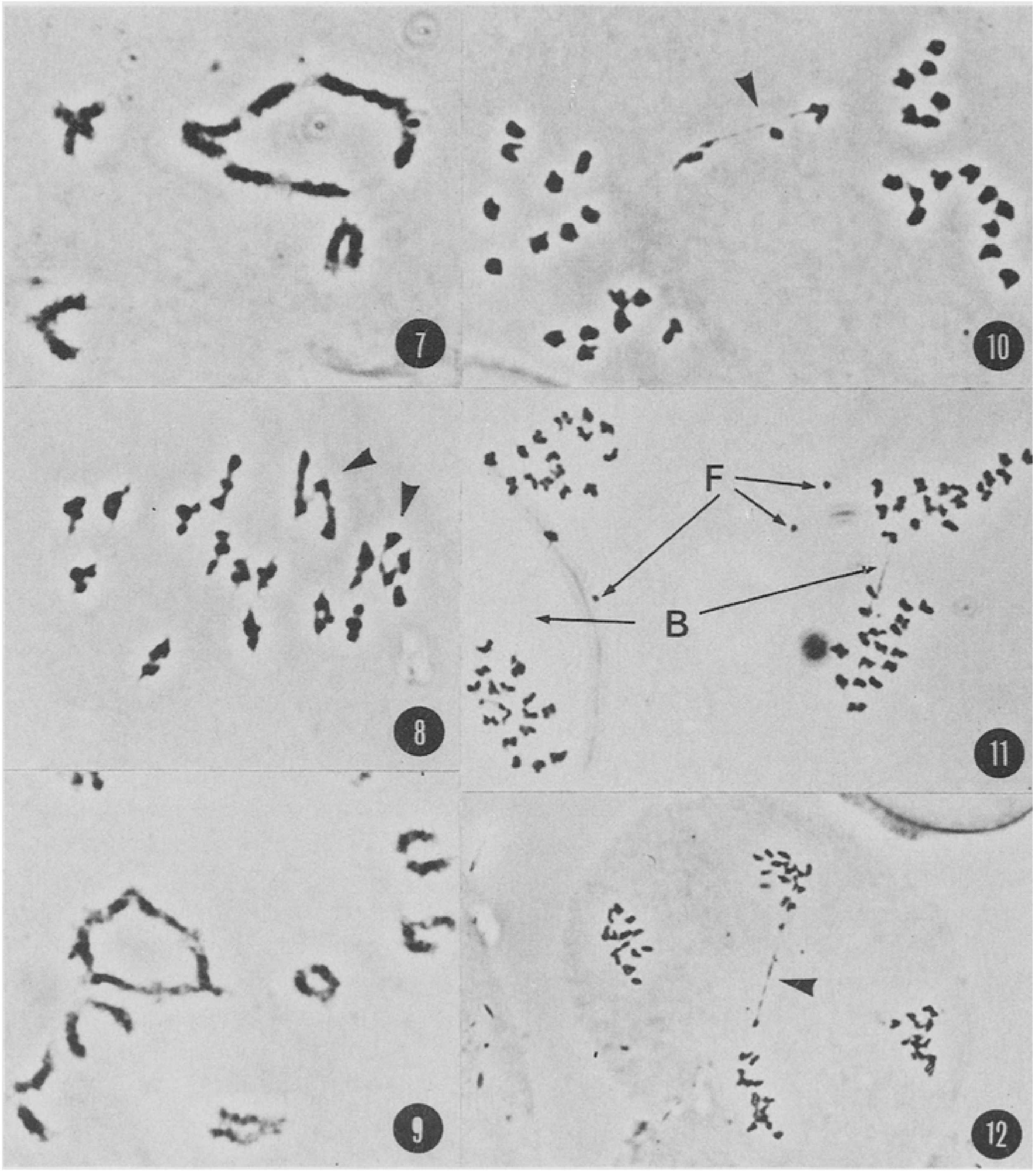
Karyotype - the number and appearance of a set of chromosomes

H. annuus

H. argophyllus

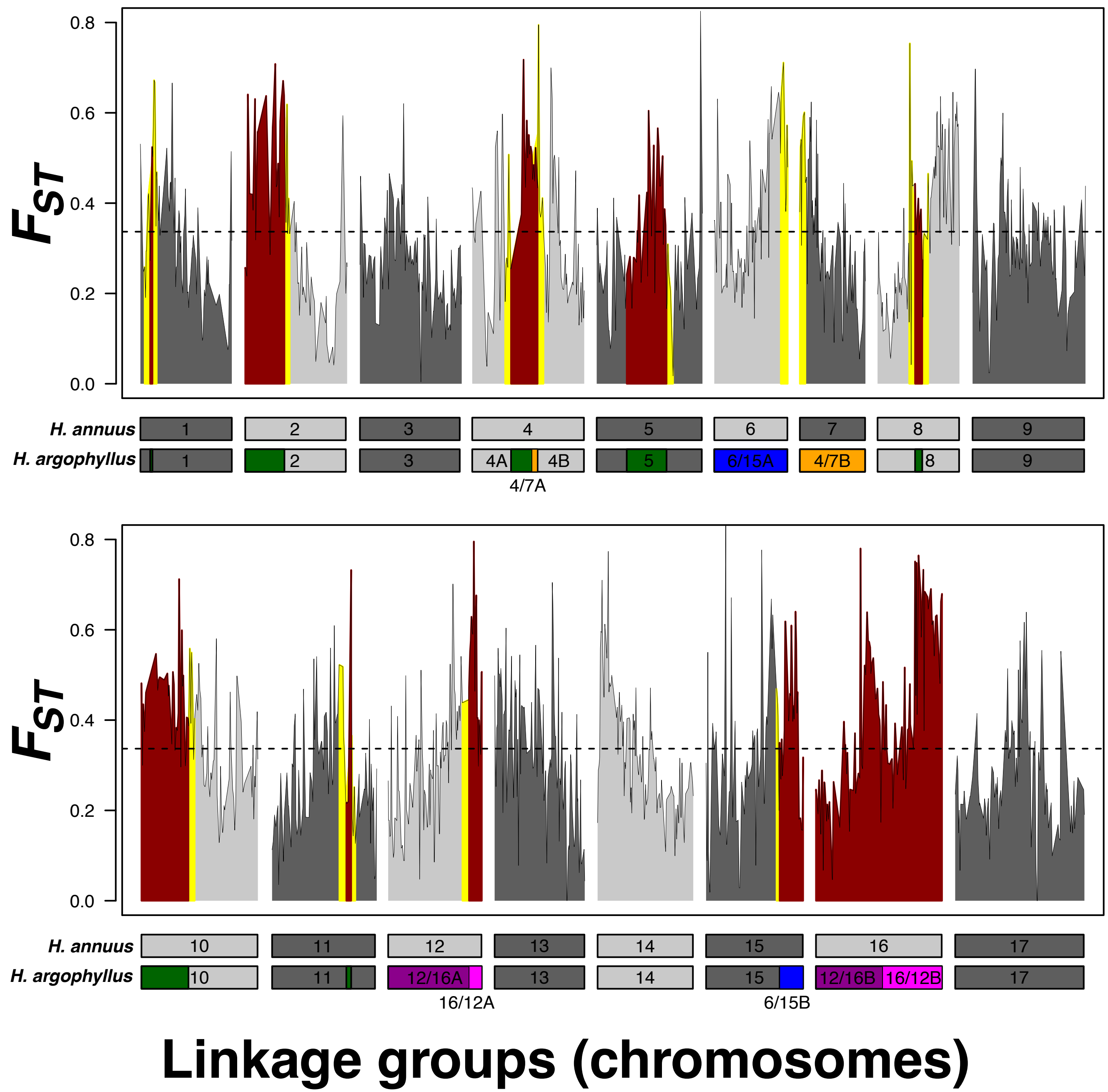
Species range and phylogenetic relationship



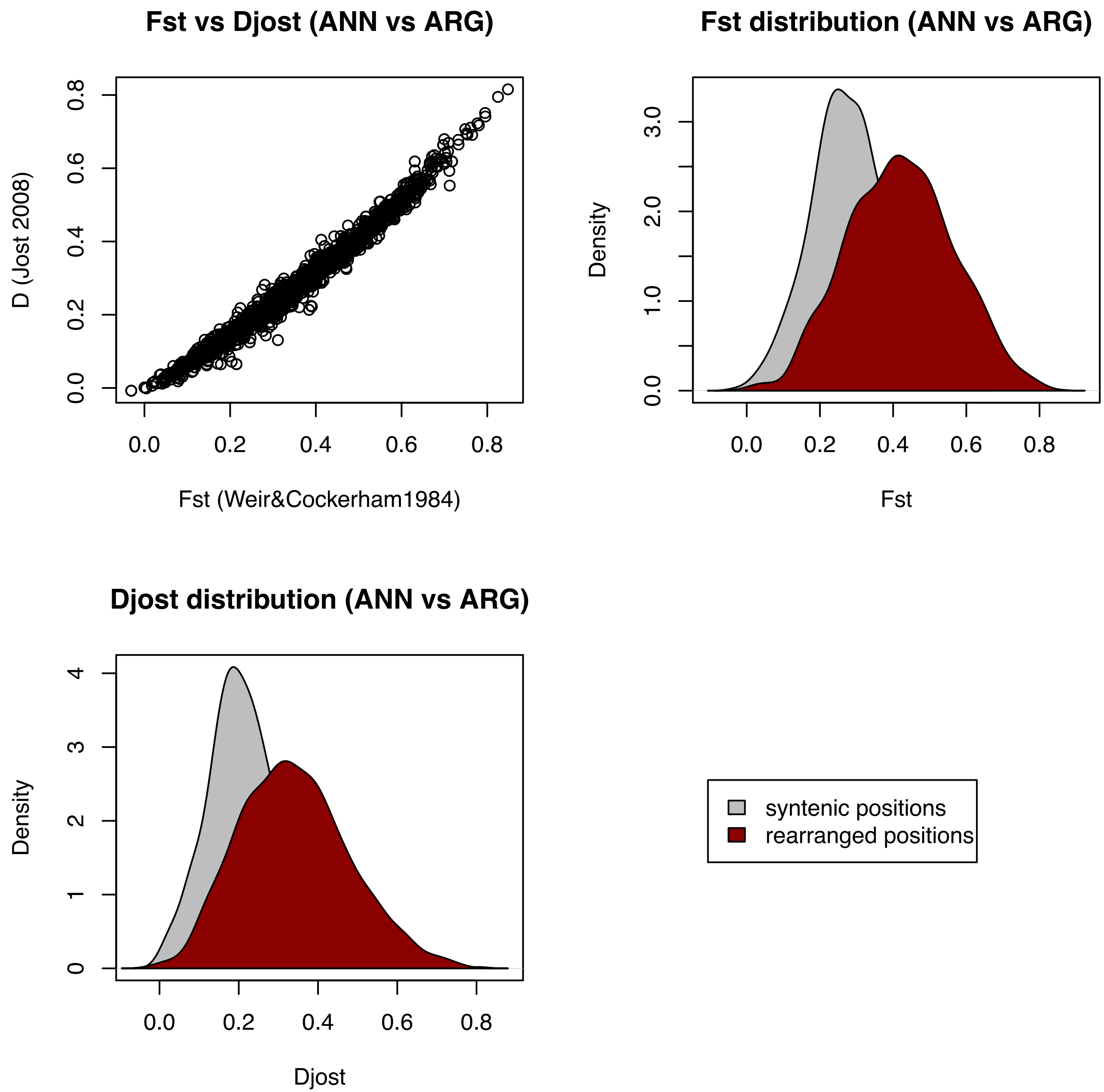


Meiotic abnormalities in hybrids between *Helianthus* species. First generation hybrids typically exhibit >90% inviable pollen.

Chromosomal and genetic differentiation between two *Helianthus* species (Barb et al. 2014)



Genetic differentiation is higher on rearranged chromosomes



Clarkia biloba

Clarkia lingulata

- Differ by a reciprocal translocation and two paracentric inversions
- *C. lingulata* 2n=9 whereas *C. biloba* 2n=8
- Hybrids are readily made, but have near-complete sterility

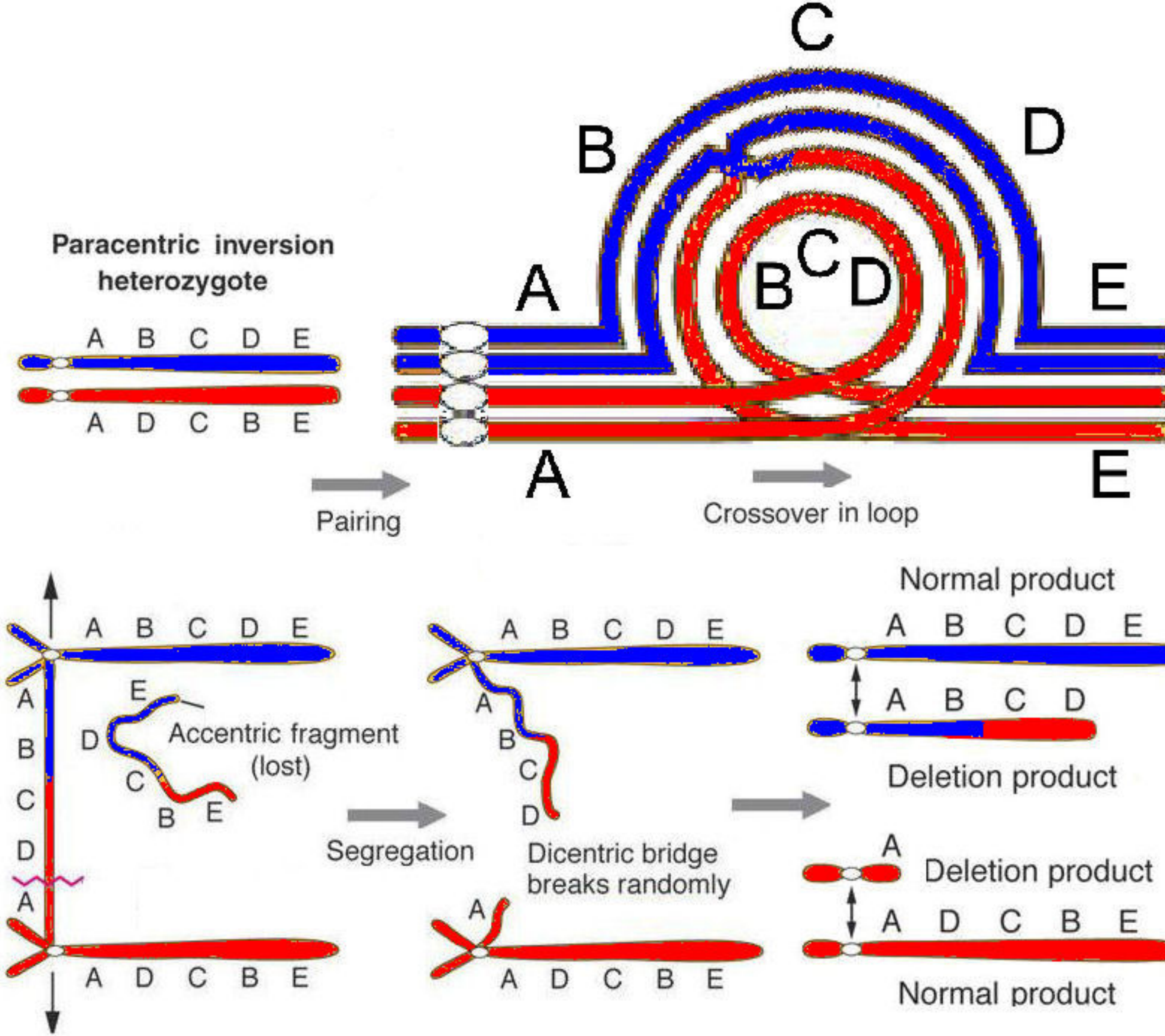
Types of Rearrangements

1. Inversions
   - paracentric (centromere outside inversion)
   - pericentric (centromere inside inversion

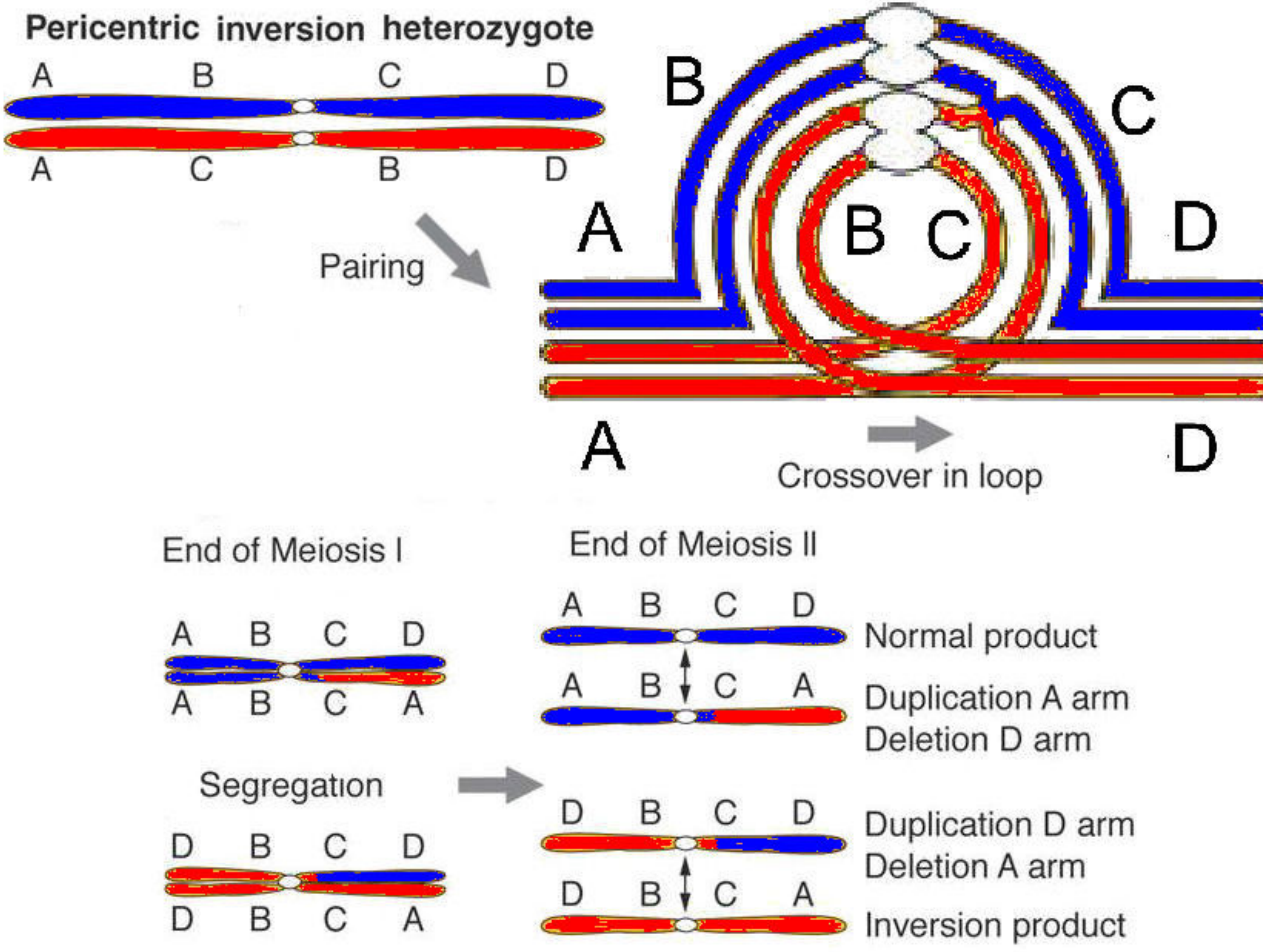
A B C D E o F G H → A D C B E o F G H

or

A B C o D E F → A E D o C B F

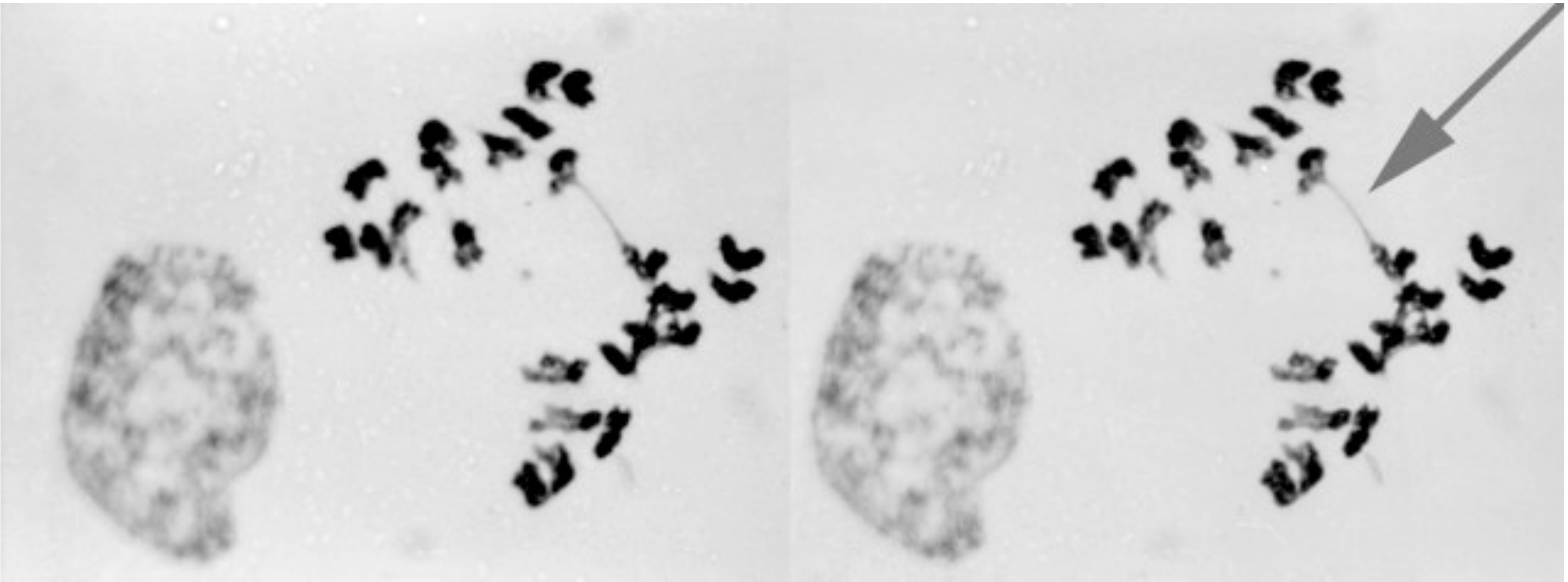


Paracentric inversion heterozygote
A B C D E
A D C B E
Pairing
A B C D E
B C D
A E
Crossover in loop
A B C D E
A B C D E
Accentric fragment (lost)
E D C B E
Segregation
Dicentric bridge breaks randomly
A B C D
A
A D C B E
Normal product
A B C D E
A B C D
Deletion product
A
Deletion product
A D C B E
Normal product



Pericentric inversion heterozygote
A B C D
A C B D
Pairing
B C
A B C D
A D
Crossover in loop
End of Meiosis I
A B C D
A B C A
Segregation
D B C D
D B C A
End of Meiosis II
A B C D
Normal product
A B C A
Duplication A arm
Deletion D arm
D B C D
Duplication D arm
Deletion A arm
D B C A
Inversion product

What kind of rearrangement is responsible for meiotic abnormality seen below?



Heslop-Harrison 2013

Types of Rearrangements

1. Inversions (continued)

Fertility effects

- up to 50% of gametes carry duplications or deficiencies
- may be compensatory mechanisms
  - (a) in Drosophila recombinant products shunted into polar bodies
  - (b) In deer mice abundant pericentromeric heterochromatin reduces crossing over

Recombination effects

- recombination suppressed within inverted region

Types of Rearrangements

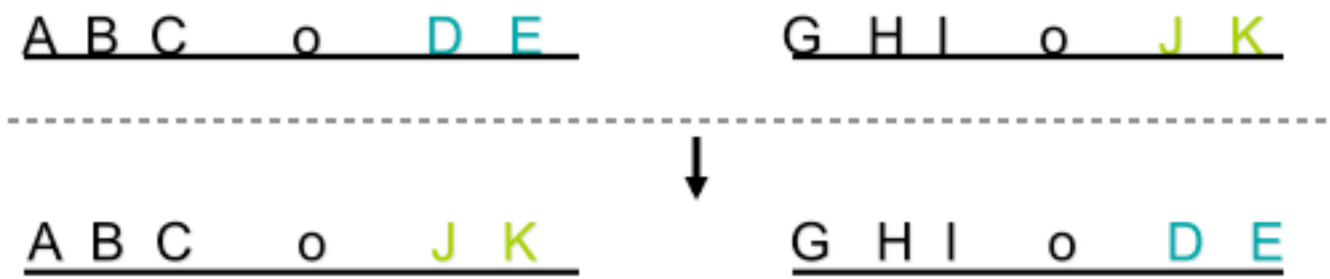
2. Chromosome fusions / fissions

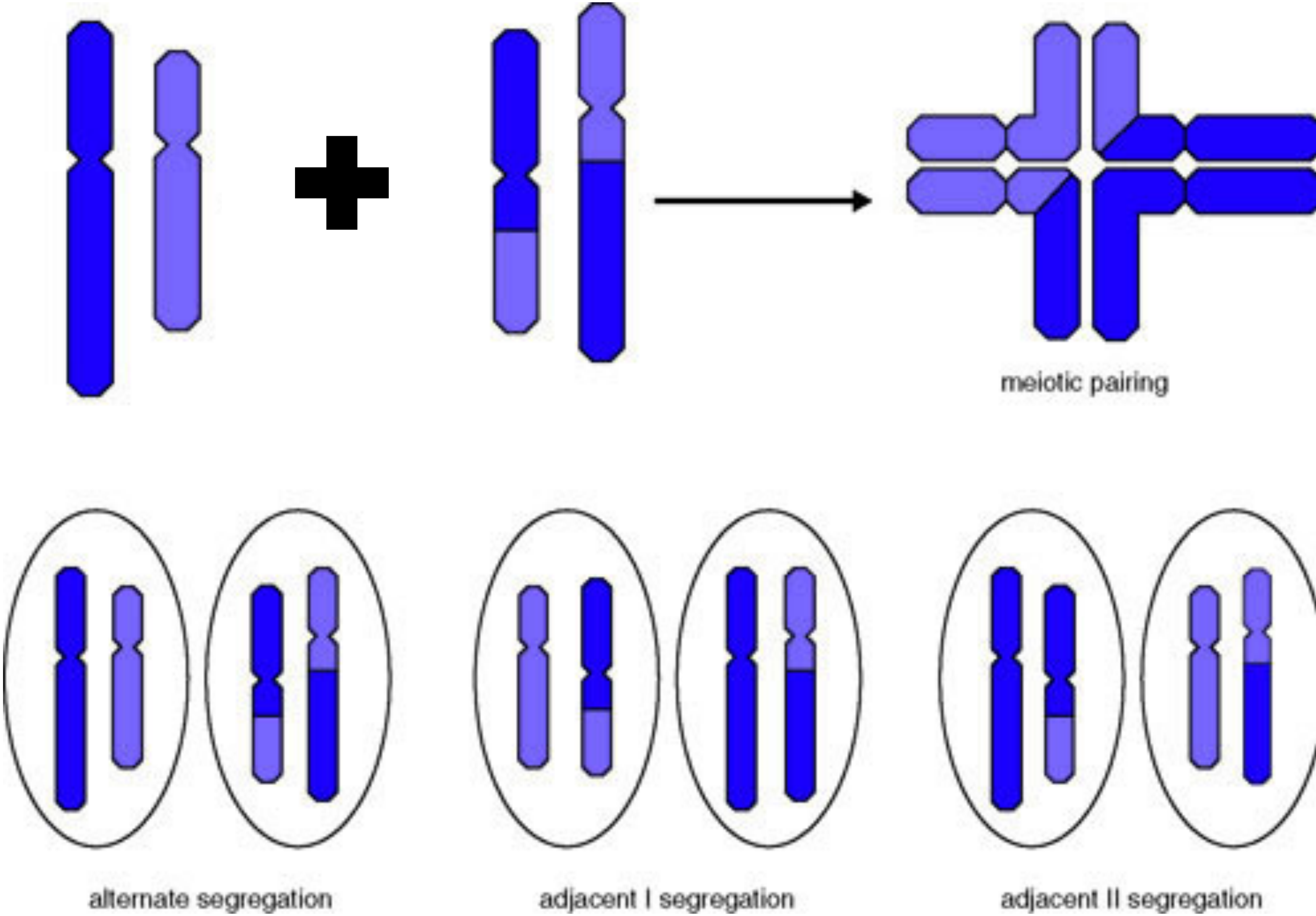
Fertility effects
- none to mild

Recombination effects
- none expected

Types of Rearrangements

3. Translocations
   - reciprocal
   - nonreciprocal





Predicted meiotic pairing in translocation heterozygote

Types of Rearrangements

3. Translocations con't

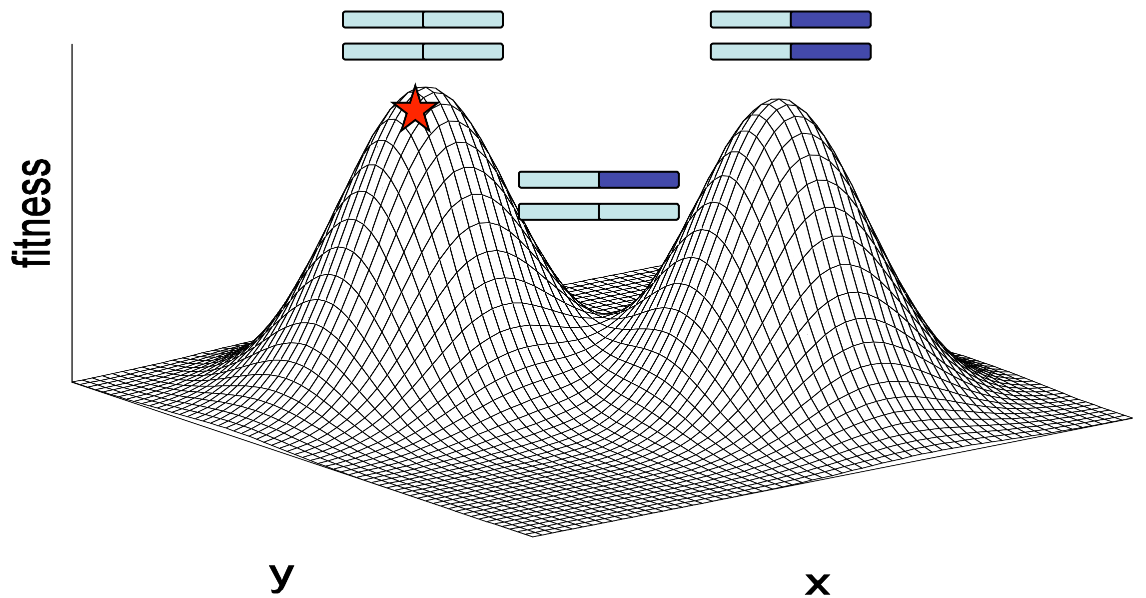
Fertility effects

- up to 2/3 of gametes will carry duplications or deficiencies
- fertility effects slightly mitigated in some plant species by non-random meiotic configurations

Recombination effects

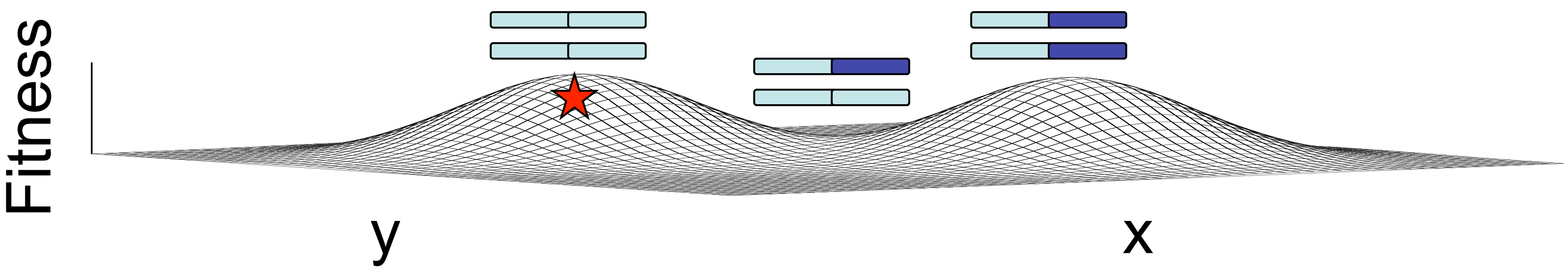
- recombination suppressed near centromere
- considerable recombination in distal regions of chromosomes

How can karyotype diverge?



-Strong underdominance (heterozygotes < fit than homozygotes)
-Establishment difficult
-Strong reproductive barrier

How can karyotype diverge?



Weak underdominance
-Establishment easier
-Weak reproductive barrier

How can karyotype diverge?

paradox: strong underdominance - establishment unlikely
weak underdominance - weak reproductive barrier

1. Drift (small population size, founder effects, kin founding)
   - Unlikely in outcrossers: fastest rates of chromosomal evolution recorded in taxa with very large populations (**Strasburg and Rieseberg 2008**)

2. Selection/migration balance (selection for multiple locally adapted alleles will favor establishment of rearrangements that limit recombination among them)

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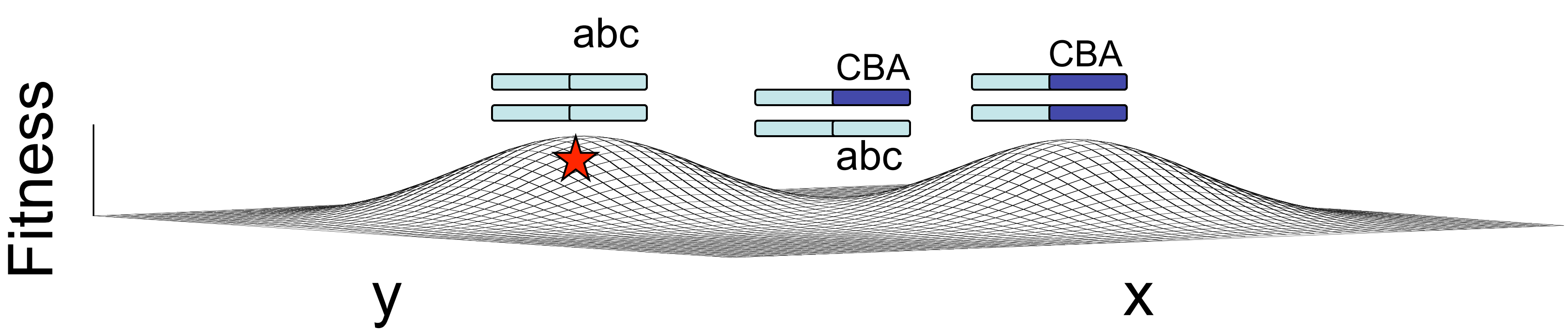
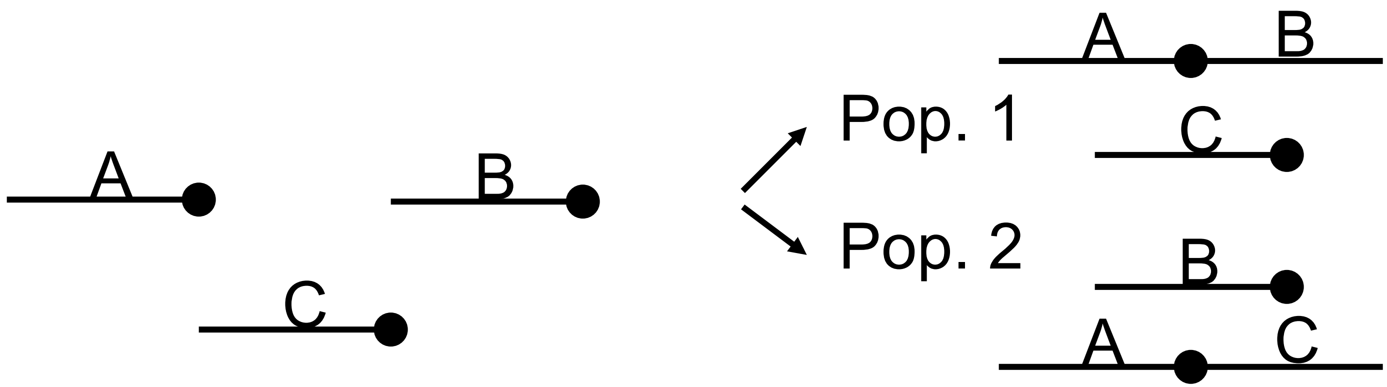


How can karyotype diverge?

3. Rearrangements weakly underdominant individually but strongly underdominant in combination (chromosomal fusions)



Ancestral population

Derived populations

How can karyotype diverge?

4. Meiotic Drive

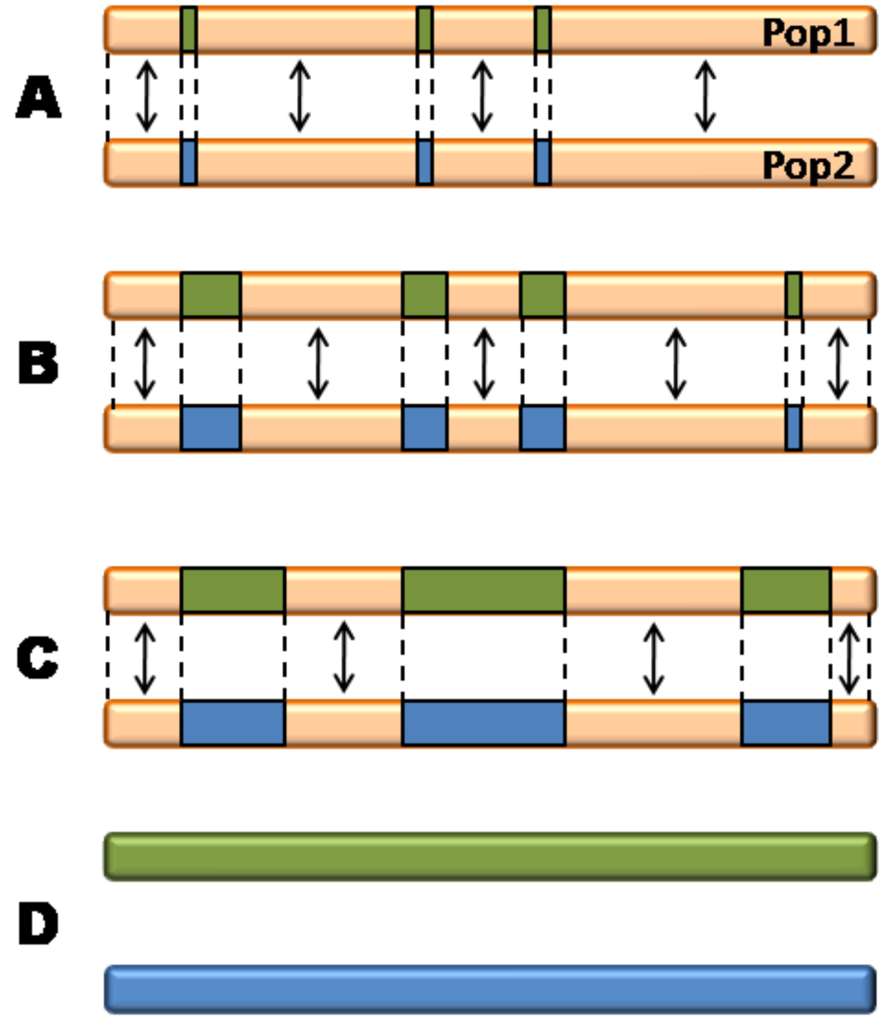
Genic Drive - an interaction between two genetic elements—a drive allele and a target locus—disables a large proportion of gametes carrying a sensitive target allele.

Chromosomal Drive - chromosomal drive, some property of the general structure or size of a chromosome bestows upon it a replication or orientation advantage.

Chromosomal Rearrangements as Recombination Modifiers

Reduced recombination may:

1) Increase size of region protected from gene flow



Stages in Speciation

Chromosomal Rearrangements as Recombination Modifiers

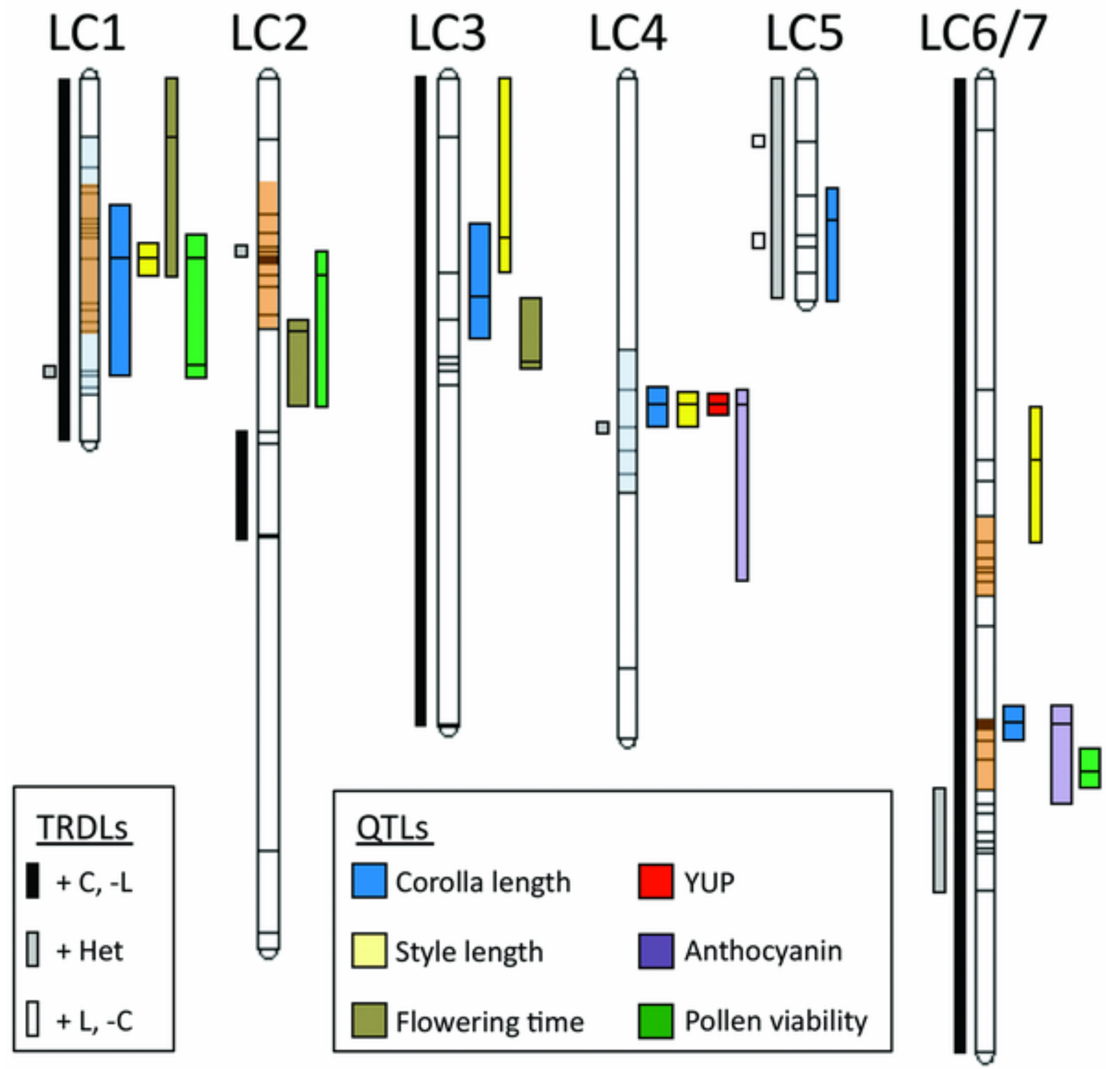
Reduced recombination may:

2) Facilitate accumulation of hybrid incompatibilities (or other species differences) in the presence of gene flow

3) Promote sympatric or parapatric speciation by creating associations between alleles under divergent natural selection and those that cause assortative mating

Chromosomal Rearrangements as Recombination Modifiers

Chromosomal rearrangements and reproductive isolation in Mimulis (Fishman et al. 2013)



Unanswered Questions

- What are the effects of translocations on recombination recombination rates?
- Is chromosomal drive common?
- How frequent are small-scale chromosomal rearrangements in plant evolution?