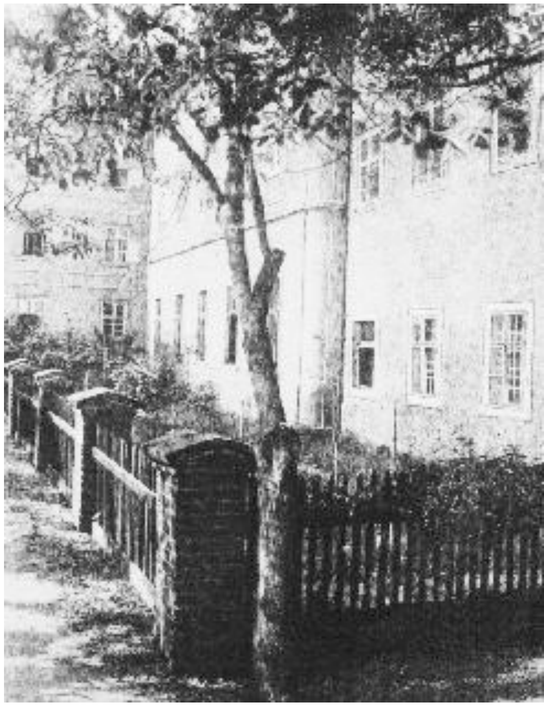
Mendel: Darwin's Savior or Opponent?

Gregor Mendel



An Augustinian monk, Mendel studied physics and natural science in Vienna, but lived most of his adult life in the cloister at Altbrunn (now Brno in the Czech Republic)

Starting in 1856 he conducted plant breeding experiments in the cloister's garden

Clicker Question

What was Mendel’s objective in carrying out breeding experiments?

- To repudiate Darwin’s theory of natural selection
- To defend Darwin’s theory of natural selection
- To identify the laws governing the formation of hybrids
- To determine how to grow peas that produced more offspring

Clicker Question

Why did Mendel elect to work with peas?

- He was interested in producing better varieties of peas
- They exhibited useful characteristics such as well-differentiated traits and protection from foreign pollen
- Different varieties exhibited different colored seeds and leaves
- They were relatively inexpensive so could be grown on a monks salary

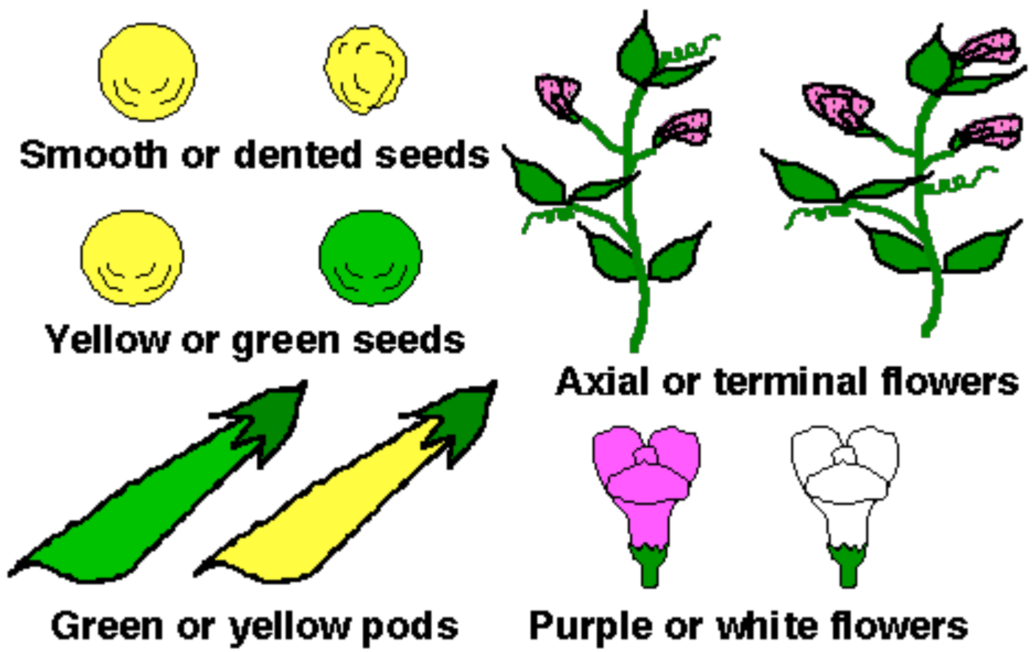
Mendel’s Breeding Experiments

An lucky choice of model organism. Chose to study peas because

They exhibit relatively easy to distinguish traits

They naturally self pollinated but are easy to cross-pollinate

To characterize their behavior in crosses, Mendel introduced the vocabulary of *dominant* (traits that appeared in hybrid crosses) and *recessive* characters (one’s that only appeared in subsequent generations)



Mendel's Procedure

- Began by cross-pollinating between pure breeding lines with alternative traits—yellow/green, smooth/dented
  - Found that all members of the F1 generation exhibited the dominant traits
    - tall rather than short stem
- Allowed members of the F1 generation to self-pollinate, generating the F2 generation
  - And analyzed the numbers exhibiting the dominant and recessive traits

F2 Generation Created from Hybrids

Form of seed	**Round / Wrinkled**	**5474**	**1850**	**2.96:1**
Color of albumin	**Yellow / Green**	**6022**	**2001**	**3.01:1**
Color of seed coat	**Violet flowers / White flowers**	**705**	**224**	**3.15:1**
Form of pods	**Inflated / Constricted**	**822**	**299**	**2.95:1**
Color of unripe pods	**Green / yellow**	**428**	**152**	**2.81:1**
Position of flowers	**Axial / terminal**	**651**	**207**	**3.14:1**
Length of stem	**Long / short**	**787**	**277**	**2.84:1**

F3 Generation

- Produced by self-pollination of members of the F2 generation

- When members of the F2 generation were allowed to self pollinate
  - Individuals with recessive traits bred pure
  - Approximately one out of three of those showing the dominant character produced only offspring with the dominant character whereas
  - Approximately two out of three of those showing the dominant character produced offspring with both the dominant and recessive character

- Theoretical problem for Mendel—what could explain these and other patterns Mendel found?

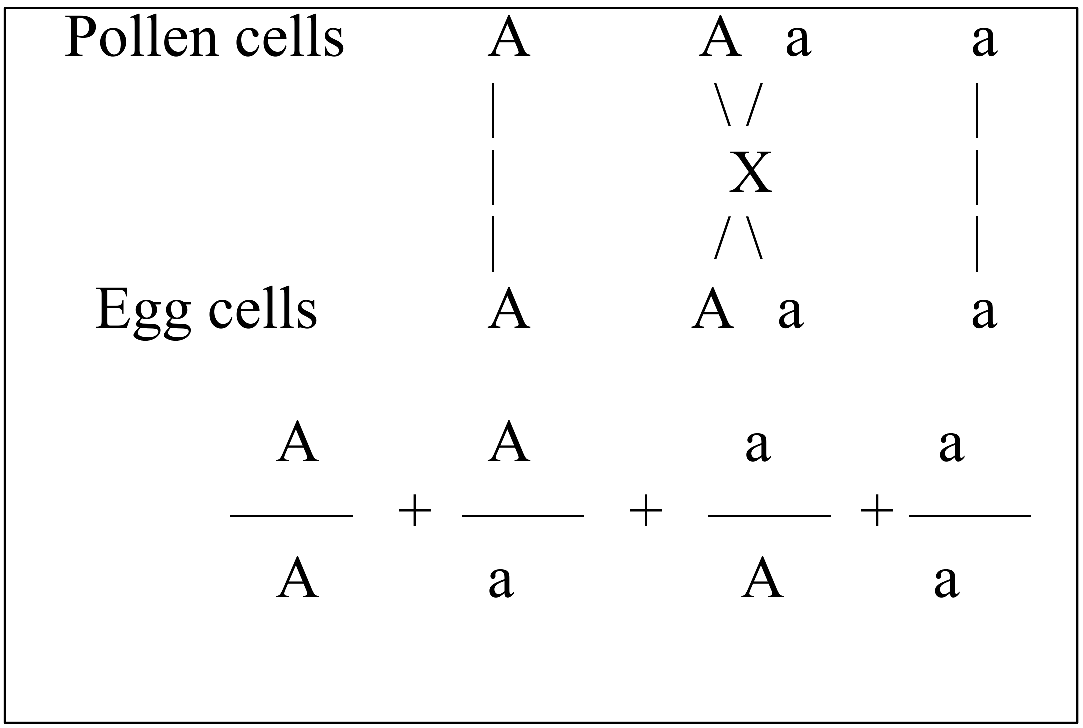
Discussion Question

When Mendel represents the results of his crosses and dominants with recessives, he writes the expression A + 2Aa + a rather than the now familiar AA + 2Aa + aa. What might account for this?

- He thought it would be wasteful to write both letters when they duplicated each other
- He was representing the characters that would be produced in offspring, not genes or factors
- His mathematics was flawed—he didn't realize that two A and two a would be produced
- He had a very different understanding of the genetics than we have today

Mendel’s Hypothesis

- Having started with the observations of the inheritance of characters, Mendel shifts to advancing a hypothesis of what accounts for the distribution of characters he observed
- He now uses A and a to refer to types of pollen and egg cells and analyzes how they might be combined:



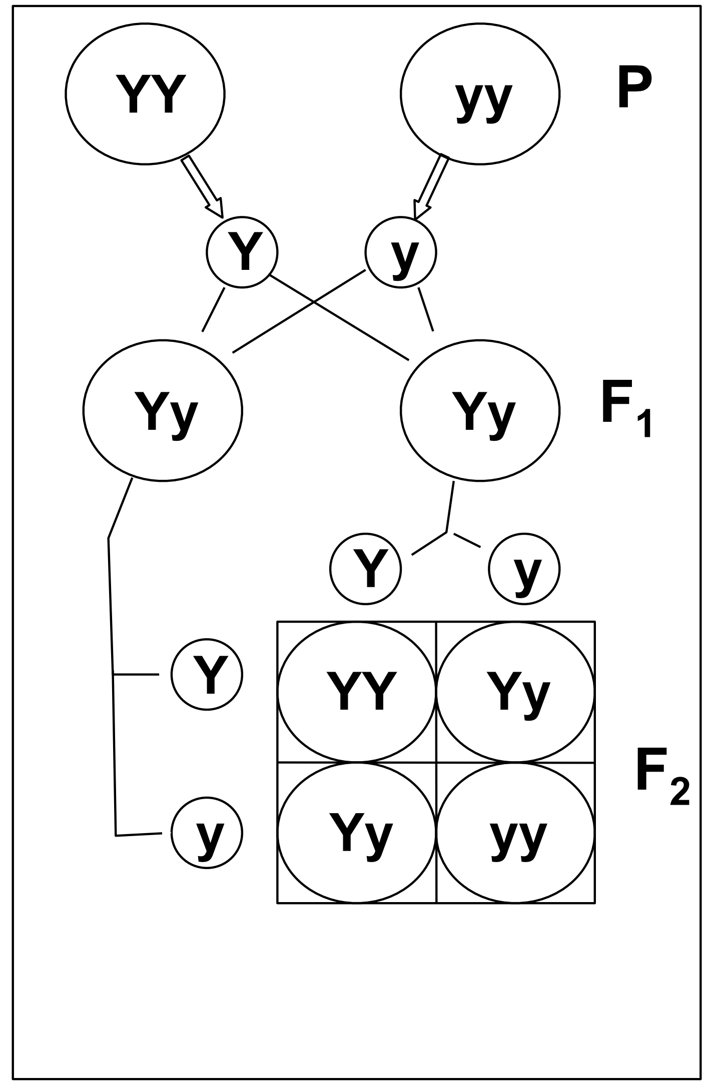
Mendel's Hypothesis (in modern terms)

Proposed that behind the characters lay *factors*

Pollen and egg cells each possessed the factor for either the dominant or recessive trait

What evidence does Mendel have for these factors?

Only that they could account for the inheritance pattern he saw and others he predicted



Mendel's "Laws"

- Three laws commonly attributed to Mendel:
  - ***Law of segregation***
    - Only one of a pair of alternative traits will be passed on through a gamete
  - *Law of independent assortment*
    - Different traits are inherited independently from each other
  - *Law of dominance*
    - One trait will "dominate" over the other in hybrids

Response to Mendel

- Presented results first at meeting of Brünn Natural History Society in 1865
- Paper was published in the Society's Proceedings in 1866
- No comments on the paper; very few citations over next 35 years
- Why neglect of Mendel?
  - Mendel in contact with Karl von Nägeli, but Nägeli's focus was different
  - Nägeli directed Mendel to work on Hawkweed, which unbeknownst to them, reproduced both sexually and asexually.
- Mendel did (could do) little to promote his results
  - Elected abbot of one of the richest cloisters in the Hapsburg Empire and spent much of the rest of his life in battle over taxation of the monastery—"Fight for the Right"

Clicker Question

In the 50 years after the *Origin*, which of these was a major question for biologists?

- Whether species evolved from prior species or were each specifically created
- Whether factors other than natural selection, such as inheritance of acquired characteristics, could explain evolution better
- Whether geological divisions between the habitats of species promoted speciation
- Whether offspring represented a blending of the traits of the parents

Clicker Question

When researchers rediscovered the work of Mendel at the beginning of the 20th century, why did they construe it as presenting an alternative to Darwinian natural selection?

- Mendel never discussed evolution, so it was reasonable to assume that he did not believe in it
- Mendel never discussed natural selection, so it was reasonable to assume that he did not believe in it
- Change in Mendelian factors/characters seemed to produce evolutionary jumps, not gradual changes
- They rejected the eugenics program embraced by the Biometrians who defended Darwinian natural selection

Rediscovery of Mendel in 1900

- Carl Correns (1864-1933) in Germany
  - Student of Nägeli, Mendel’s main correspondent (who led Mendel to study hawkweed)

- Hugo De Vries (1848-1935) in Netherlands
  - Had been conducting experiments inspired by Darwin’s account of pangenesis in the 1890s and from his observations reconstructed Mendel’s laws

- Erich Tschermak von Seysenegg (1871-1962) in Austria
  - Grandfather had taught Mendel botany!

Mendelism as an Alternative to Natural Selection

- De Vries' Mutation Theory
  - De Vries has observed evening primrose colonies outside Amsterdam in 1900
  - Offspring often differed dramatically from their parents
    - Termed these different offspring "mutations"
    - (Actually due to chromosome duplications)
  - Interpreted mutations as producing different species
    - Fast
    - No expectation of intermediate forms

An Uncelebrated Visit to San Diego

- In the month of June 1906, San Diego was visited by one of the greatest scientists of that time. His arrival was announced in the list of guests of the Coronado Hotel for 4 June 1906, where he was listed as Col. Hugo de Vries, Amsterdam. The "Col." cannot be a southern title, for Hugo de Vries never visited Kentucky, nor was he ever in military service. Except for this announcement, his visit went unnoticed. Nobody apparently greeted him at the railway station, nobody acted as his *Cicerone.* Alone, he wandered over San Diego's hills and the *mesa,* enjoying the plants which grew there and admiring the view.

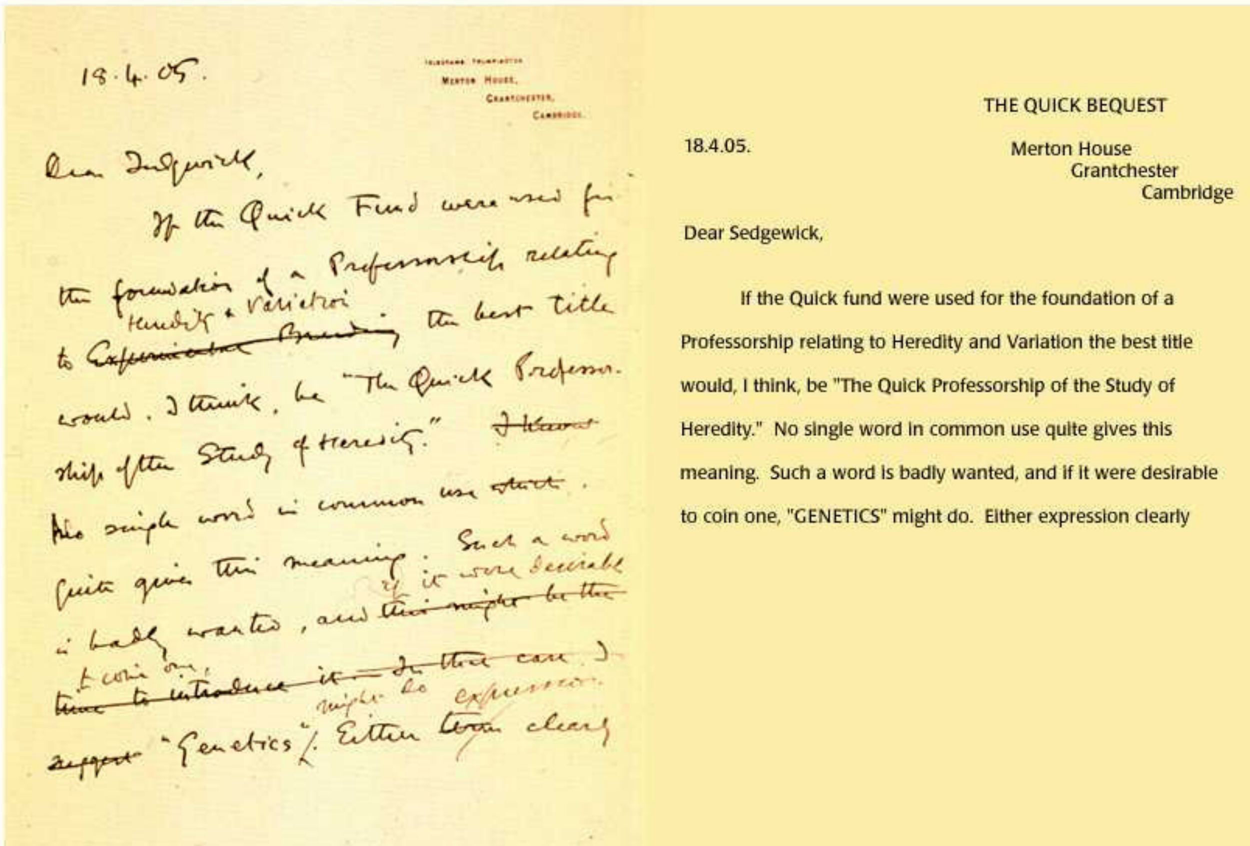
    HUGO DE VRIES VISITS SAN DIEGO

    By Peter W. van der Pas, *Journal of San Diego History, 1971*

Arbitrating the Priority Dispute

- William Bateson in England focused his evolutionary research on discontinuous variations
  - Bees with legs where there should be antennae
  - Humans with six fingers or extra ribs
- Was not one of the rediscovers of Mendel, but he got to settle the priority dispute by naming the view Mendelism
- Became champion of Mendelism (saltationism) in opposition to the biometricians (who emphasized gradualism)
  - Had Mendel’s paper translated into English (1901-1902)

Bateson Offers A Name: Genetics



THE QUICK BEQUEST

18.4.05.

Merton House
Grantchester
Cambridge

Dear Sedgewick,

If the Quick fund were used for the foundation of a Professorship relating to Heredity and Variation the best title would, I think, be "The Quick Professorship of the Study of Heredity." No single word in common use quite gives this meaning. Such a word is badly wanted, and if it were desirable to coin one, "GENETICS" might do. Either expression clearly

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- *Genetics* from *genetikos*, Greek for produced
- Wilhelm Johansen in 1909 introduced the term *gene*
- Bateson also coined the terms *allelomorphs* (later shortened to *allele*), *zygote, heterozygote* and *homozygote.*

A Representational Tool: The Punnett Square

- The device for representing the genotypes that result from crosses in tables was developed by Reginald Punnett, a close collaborator of Bateson's at Cambridge
- A major contribution to making the theory intelligible

	R	**R**
R	RR	RR
r	Rr	Rr

	RY	**Ry**	**rY**	**ry**
RY	RRYY	RRYy	RrYY	RrYy
Ry	RRYy	RRyy	RrYy	Rryy
rY	RrYY	RrYy	rrYY	rrYy
ry	RrYy	Rryy	rrYy	rryy

Biometrician-Mendelian Conflict

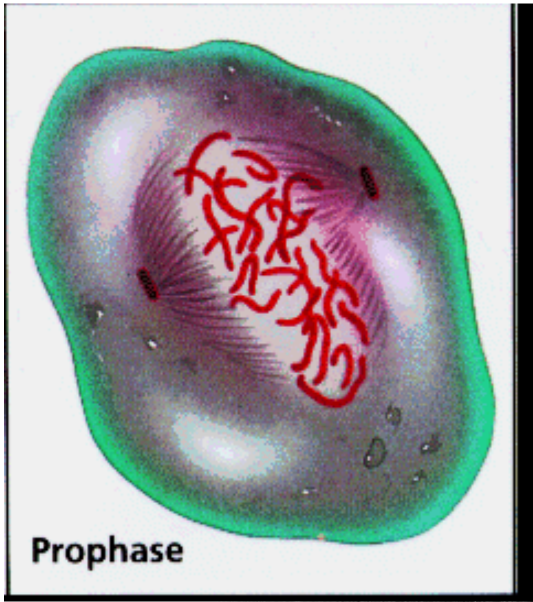
- Zoological Section, British Association, 1904
- William Bateson for Mendel
  - Cinneraria derived from hybridization in a wild population with many distinct (discontinuously-varying) varieties
- W.F.R. Weldon for Biometricians
  - Cinneraria originated through gradual selection from continuously-varying wild population (in Canary Islands)

Biometrician-Mendelian Conflict

- At stake:
  - For the Mendelians: Survival of the new field
  - For the Biometricians: continued control over "Evolution Committee" of the Royal Society (Composed of Galton, Pearson, Bateson and Weldon)

	Mendelians	Biometricians
Variation	Discontinuous	Continuous
Evolution	Rapid, step-wise	Slow, gradual
Selection	Small negative role: weeds out unfit	All-important moves mean of population in direction of selection

Linking Genes with Known Cell Structures



- For many biologists, genes (factors) were abstract, not physical, entities
- Chromosomes were identified in nucleus of dividing cells with the use of stains in the 1870s
  - Leading to studies of their role in development
- Link between Mendel's factors and chromosomes developed from work by Theodor Boveri and Walter Sutton
  - Boveri, working with sea urchins, showed that each chromosome contributed differentially to normal development
  - Sutton in 1902 proposed that chromosomes could provide the physical basis of Mendelian inheritance

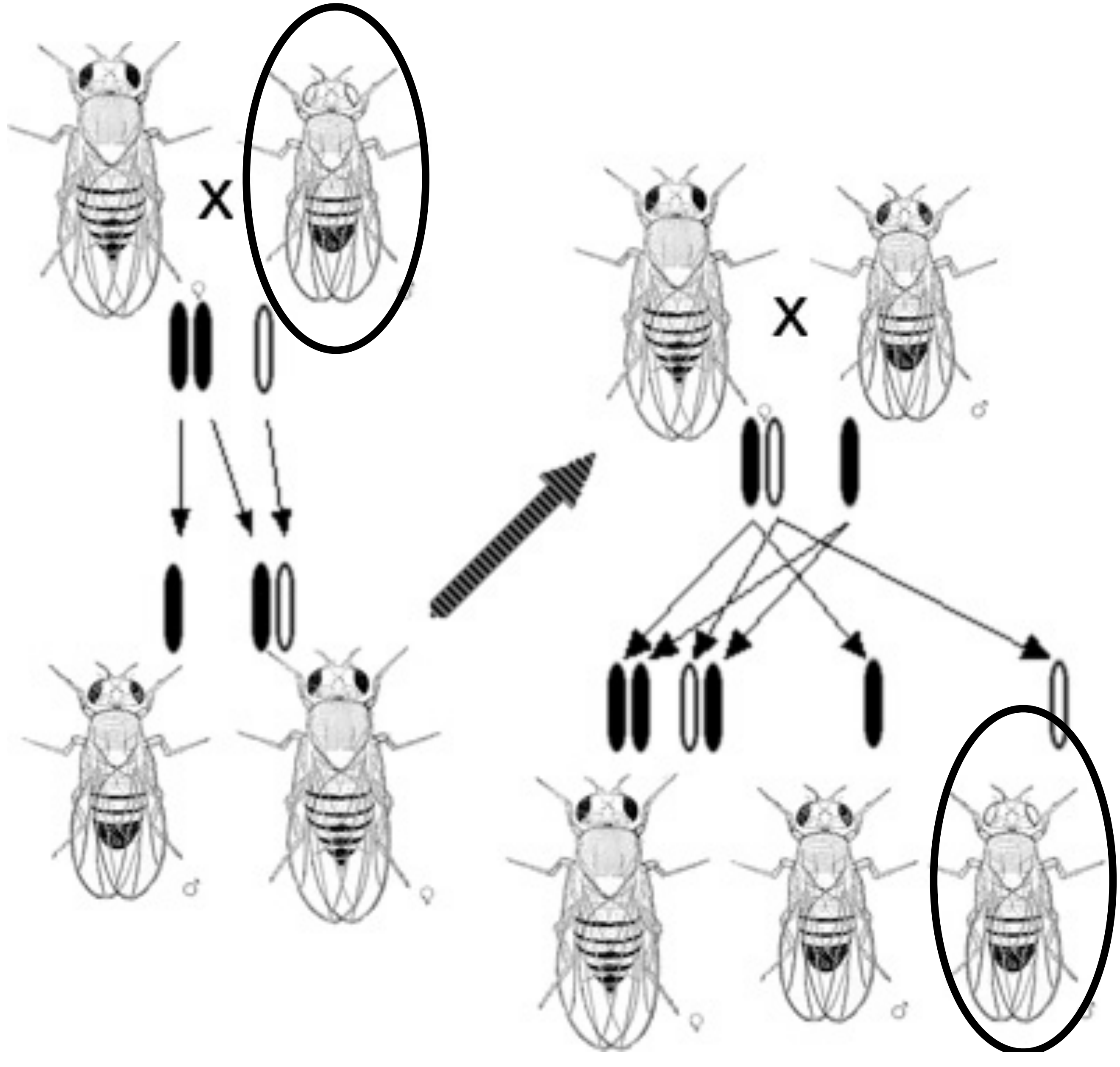
Cementing the Link: Thomas Hunt Morgan

- Morgan's initial focus was on development
  - Experimental studies of embryo formation, e.g., formation from separated blastomeres or in different salt concentrations
- Initially skeptical of both Darwinian natural selection and Mendelian inheritance
  - Bothered by the hypothetical and preformational character of Mendelian factors
  - Rejected chromosome theory: individual chromosomes did not carry hereditary information

Morgan's Conversion to Mendelism

- Observed a white-eyed mutant in 1909
  - When crossed with normal red-eyed flies, all the offspring had red eyes
  - But the next cross yielded male flies with white eyes
  - Referred to such traits as sex limited (sex-linked)
  - Discovered other sex-linked traits (rudimentary wings and yellow body color) and determined that these were all inherited together
  - Concluded that the X-chromosome carried a number of discrete hereditary units
  - Developed the chromosomal theory of inheritance

Sex-Linked Inheritance of White Eyes--1911



Thomas Hunt Morgan and the Fly Lab

- Discovered linkage groups: groups of genes that were inherited together
- Discovered crossover: paired chromosomes could exchange parts, leading to genes on different parts of one chromosome being separated in subsequent generations
- Established that the distance between genes determined probability of crossover
  - Genes further apart would be more likely to crossover
  - Rate of crossover became a tool for mapping location of genes on chromosomes
- Sturtevant developed the first genetic map in 1913
  - Discovered double crossovers

Mechanism of Mendelian Heredity

- Published with his graduate students Alfred Henry Sturtevant, Calvin Blackman Bridges, and Hermann Joseph Muller in 1915

- Bridges had established relations between crossover points and banding on the giant Drosophila chromosome allowing for the first physical mapping of genes to chromosomes