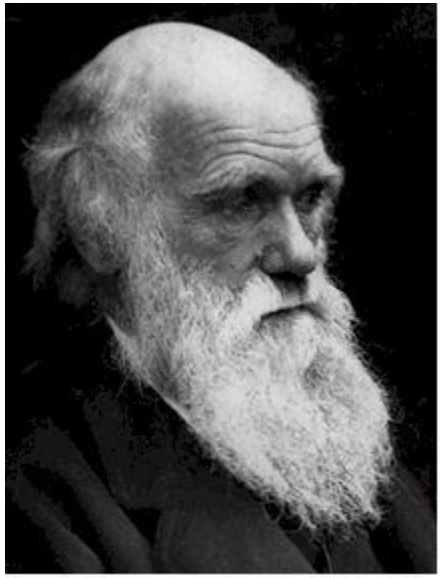
Malthus, Darwin, and Natural selection: an historical introduction to evolution

Thomas Malthus

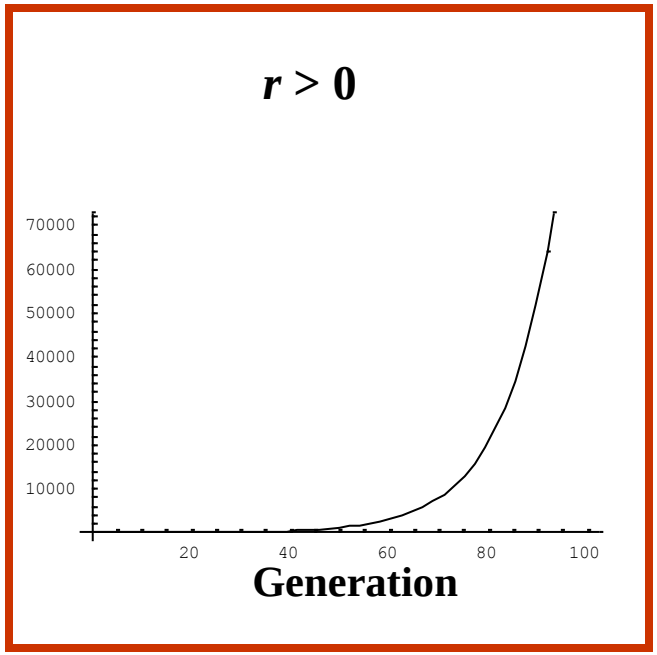


Charles Darwin

"nothing in biology makes sense except in the light of evolution"

Theodosius Dobzhansky, 1973

Malthus, Darwin, and Natural selection



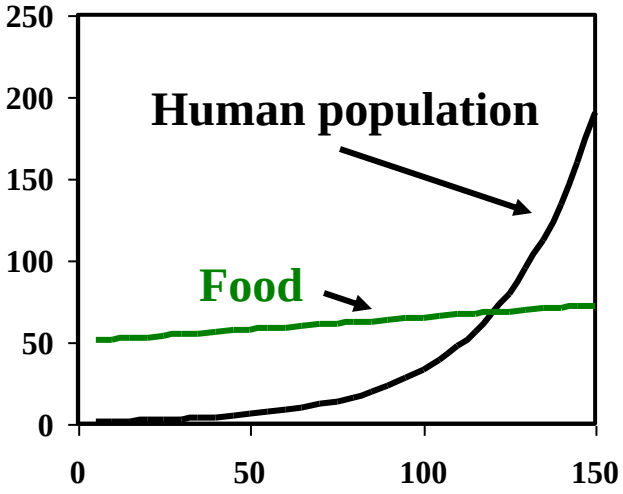
This observation inspired the economist Thomas Malthus

Thomas Malthus (1766-1834)

Thomas Malthus

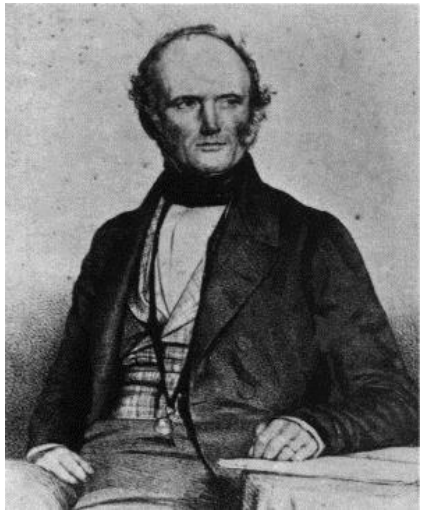
Essay on the Principles of Population, 1798.

"The power of population is so superior to the power of the earth to produce subsistence for man, that premature death must in some shape or other visit the human race"



- Argued that the food supply increased linearly while population size increased exponentially
- Malthus' writings would ultimately inspire Darwin's theory of evolution by natural selection

Before reading Malthus, Darwin had been primed by advances in geology



Sir Charles Lyell
(1797 - 1875)

- In 1830 Lyell published "The Principles of Geology: Being an Attempt to Explain the Former Changes of the Earth's Surface, by Reference to Causes now in Operation"

- Argued that those forces which generated geological change in the past are those still in operation today.

- Argued that small forces continued over long periods of time could lead to great geological changes. e.g., the Himalayas…

These geological arguments strongly influenced Darwin

And by his travels on board the Beagle (1831-1836)

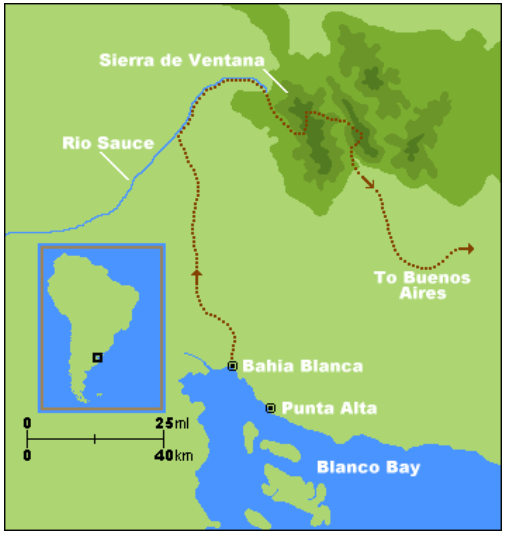
Darwin called this trip:

"...by far the most important event in my life, and has determined my whole career"

Voyage of *HMS Beagle* (1831-1836)

What did Darwin see on this journey that was so influential?

During this voyage Darwin was particularly struck by fossils



Fossil of giant ground sloth *Megatherium*

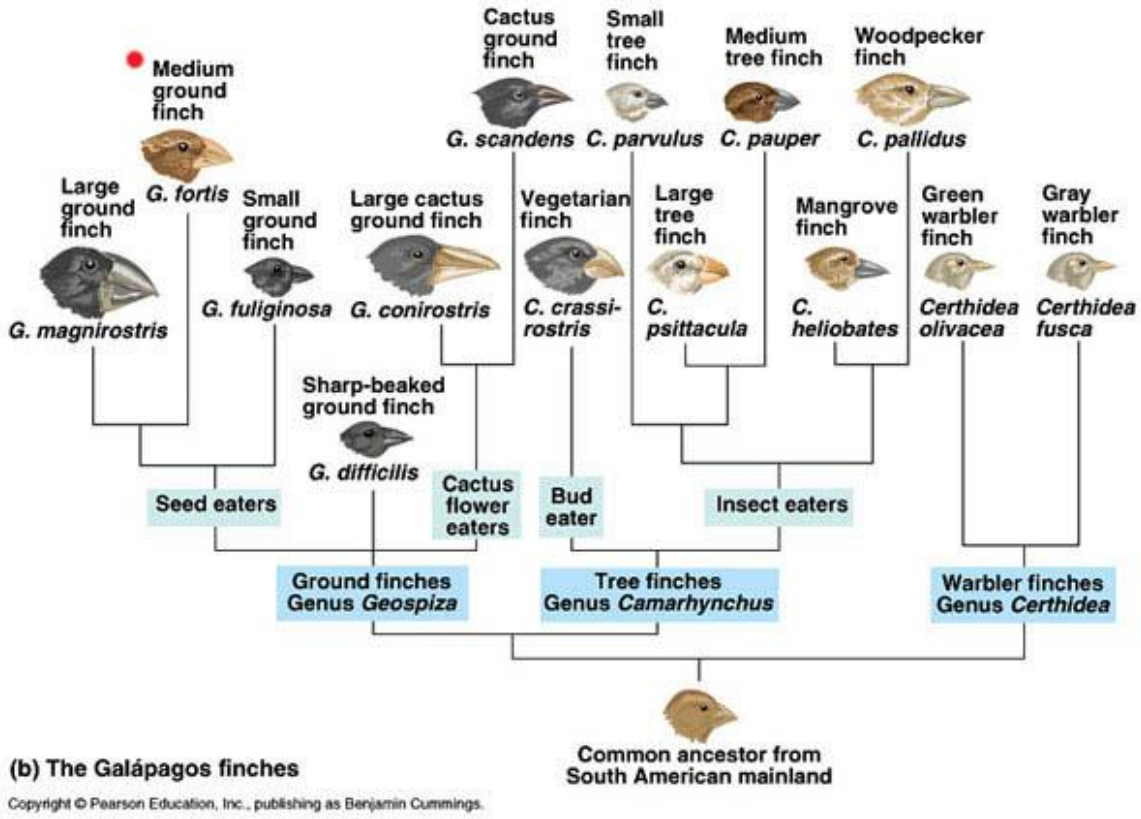
- **Darwin uncovered fossils of nine large mammals, all unknown to science. The largest of these was *Megatherium***
- **Based upon the depth of the fossil and his appreciation for Lyell's work, Darwin guessed it must have died many thousands of years before**
- **What caused the extinction of this species?**
- **Why was it similar (albeit much larger) to other extant creatures inhabiting the area?**
- **"It was evident," Darwin later wrote, "that such facts as these, as well as many others, could be explained on the supposition that species gradually become modified; and the subject haunted me."**

Darwin was also struck by the diversity of organisms on the Galapagos

"If there is the slightest foundation for evolution, the zoology of the Galapagos will be well worth examining..."

What did Darwin see on the Galapagos that influenced him?

Incredible diversity across islands



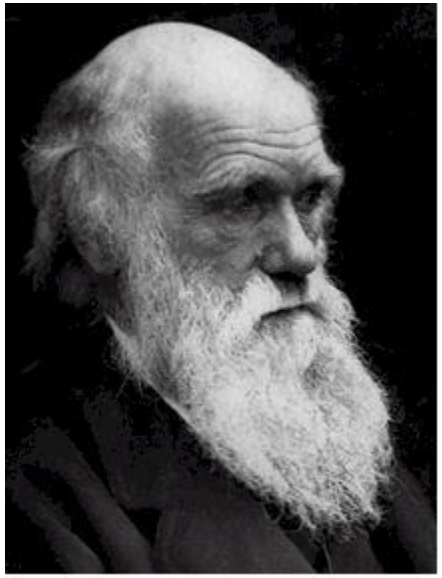
(b) The Galápagos finches

- **Although Darwin did not initially make much of the finches, he was impressed by levels of differentiation among islands (e.g., different mockingbird "varieties" or species on each island)**

- **Later, after the collected birds had been classified, Darwin realized that birds on the Galapagos must have arisen from mainland finches that had adapted to diverse island environments**

In July of 1837 one year after returning from the voyage of the Beagle, Darwin began to write down his thoughts

- **By this time Darwin firmly believed that species changed over time**
- **Darwin did not, however, have a mechanism that could explain these changes**
- **It was during this time that Darwin discovered Malthus' work**



Charles Darwin

In October 1838 … I happened to read for amusement Malthus on *Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on … it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The results of this would be the formation of a new species. Here, then, I had at last got a theory by which to work.

-- Charles Darwin, *Autobiography*

Darwin's theory of natural selection I.

- **Any species can, at least theoretically, increase its population size exponentially and indefinitely.**

- **Yet we do not see this; population size generally remains constant or at least within well defined limits.**

Darwin concluded from this that:

1. Not all offspring that are produced will survive

2. This leads to a perpetual "struggle for existence"

Darwin's theory of natural selection II.

- **Individuals within species vary**

- **Some individuals vary in ways that help them survive and/or reproduce**

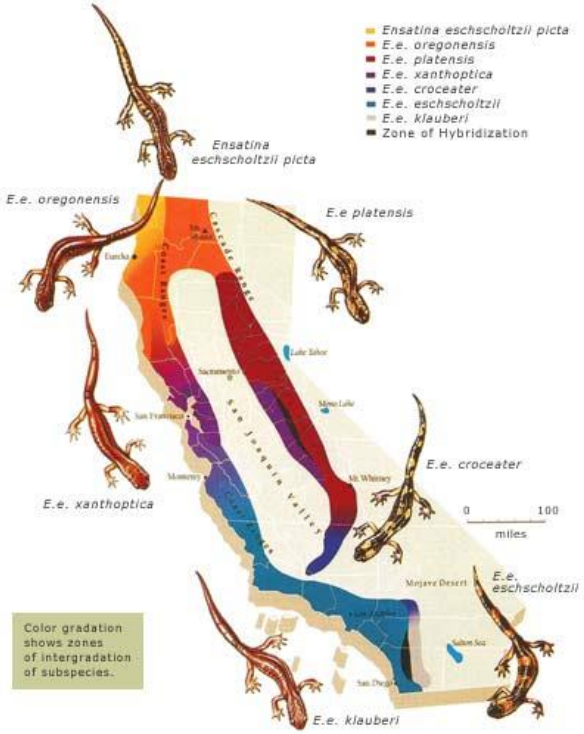
- **Variation is inherited; for whatever reason offspring resemble their parents**

From these observations, Darwin concluded that a species will change over time as favorable traits increase and unfavorable traits are eliminated.
Over time, this will tend to produce new and different VARIETIES.

Darwin's theory of natural selection III.

- It is often difficult to tell where to draw the line between a variety and a species

- There has been a virtually unlimited amount of time for changes to accumulate (Lyell)



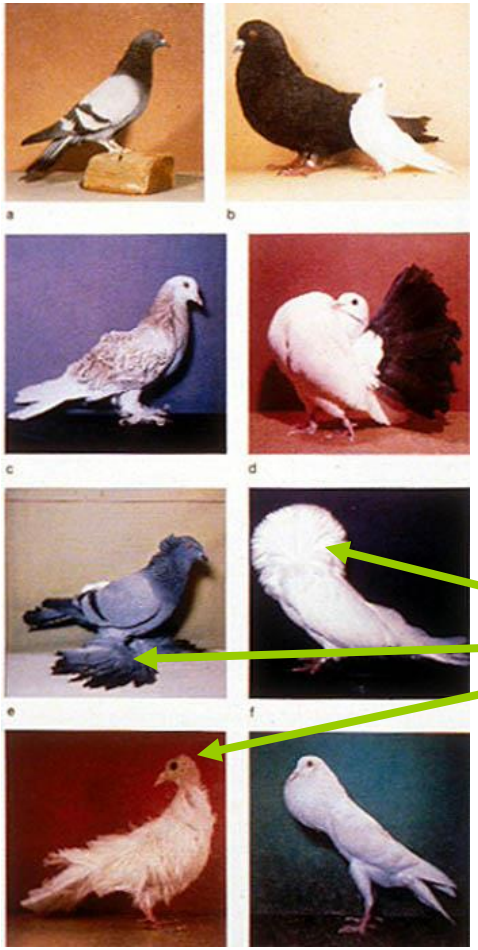
Darwin's conclusion was that the process of natural selection has, over time, created countless new species.

There were, however, two problems which plagued Darwin's theory

1. No one had ever seen natural selection in action

2. Even if natural selection did occur, how were favorable traits passed on?

Darwin spent the next 20 years gathering evidence



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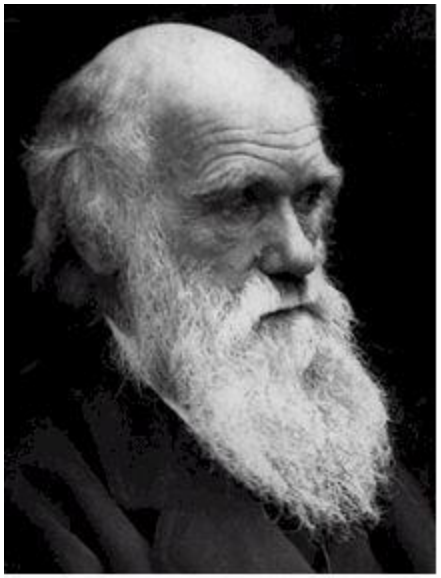
Much of his evidence derived from cases of artificial selection… like pigeons!

These examples convinced Darwin of the efficacy of natural selection

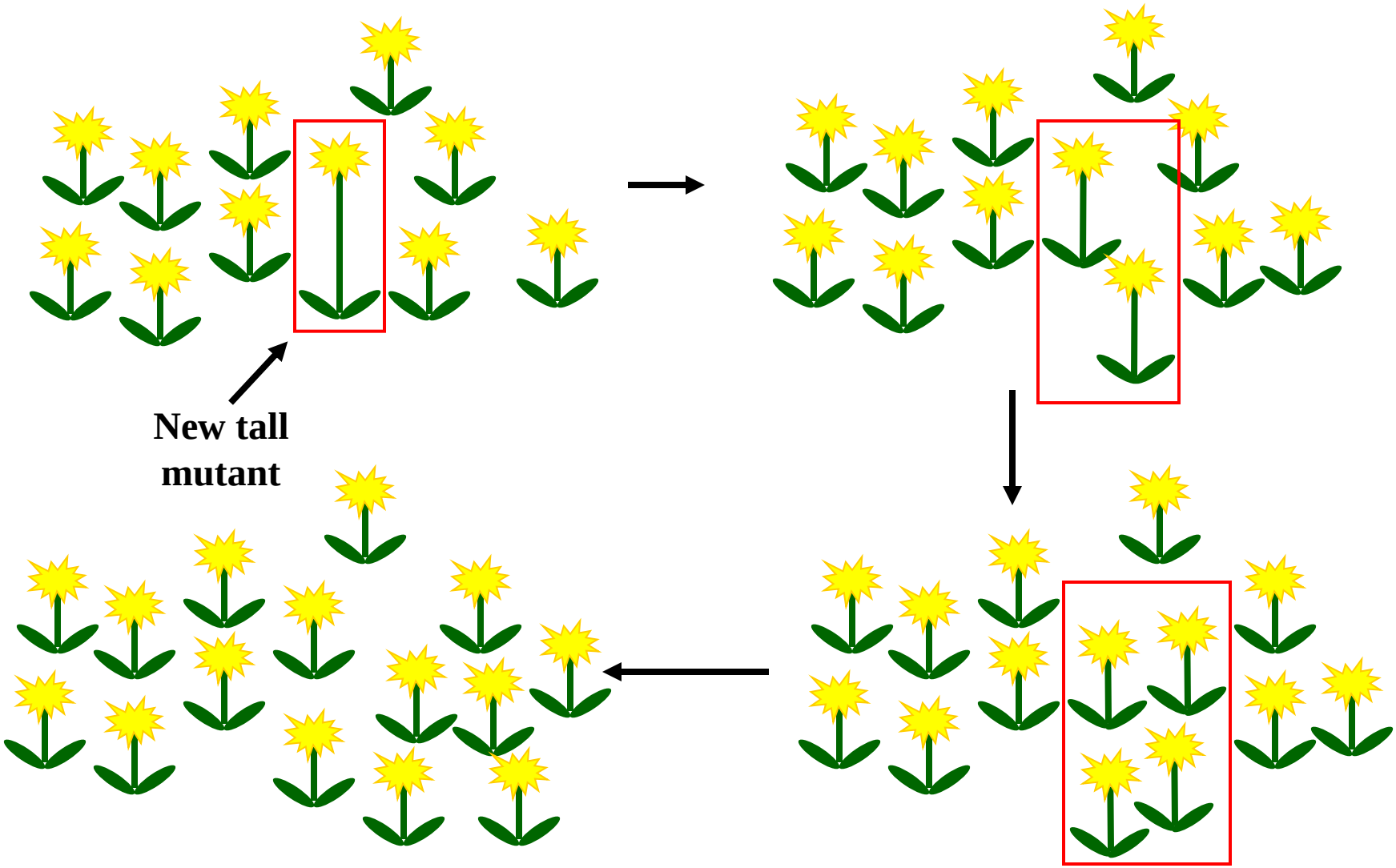


"… I determined to collect blindly every sort of fact, which could bear any way on what are species… I am almost convinced (quite contrary to the opinion I started with), that species are not (it is like confessing a murder) immutable."

-- Letter to J.D. Hooker
January 11, 1844

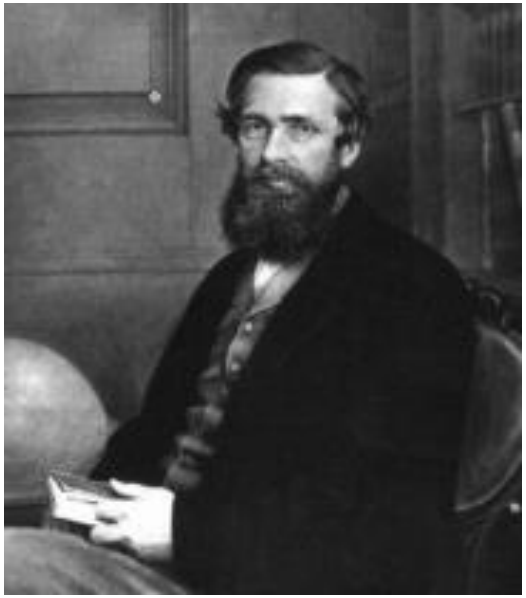
But the mechanism of inheritance remained elusive

The primary problem was ‘blending’



New favorable mutations would always be diluted!!

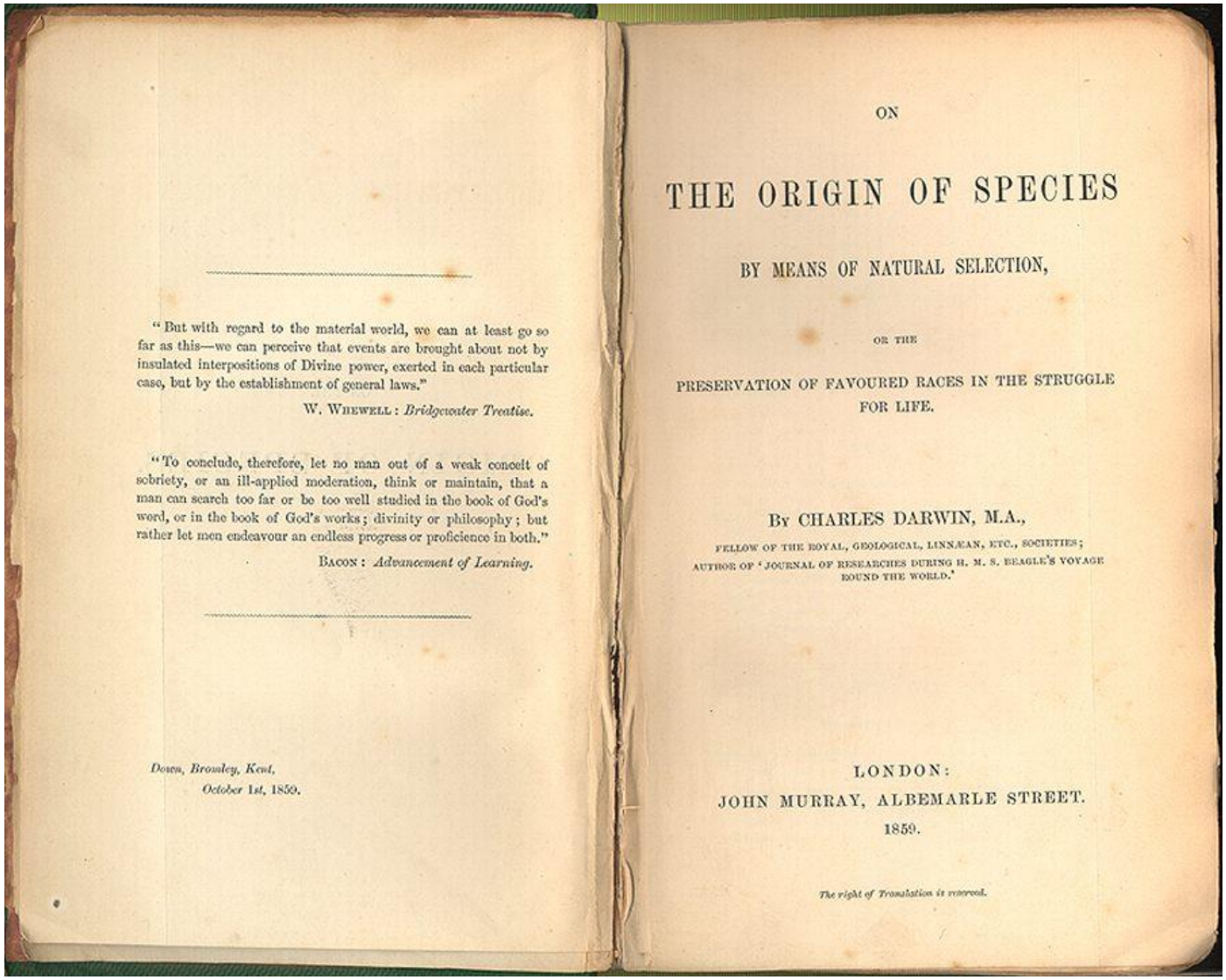
Darwin never solved this problem and ultimately was forced to publish his work by Wallace's parallel findings



Alfred Russel Wallace

- Professional collector
- Came to his parallel ideas in a malarial fever while on a collecting trip in Malaysia
- Wrote a letter to Darwin explaining his ideas which ended up being read at the next meeting of the Linnean Society along with some of Darwin's writings

In 1859, the Origin of Species was published



"But with regard to the material world, we can at least go so far as this—we can perceive that events are brought about not by insulated interpositions of Divine power, exerted in each particular case, but by the establishment of general laws."

W. WHEWELL: *Bridgewater Treatise.*

"To conclude, therefore, let no man out of a weak conceit of sobriety, or an ill-applied moderation, think or maintain, that a man can search too far or be too well studied in the book of God's word, or in the book of God's works; divinity or philosophy; but rather let men endeavour an endless progress or proficience in both."

BACON: *Advancement of Learning.*

Down, Bromley, Kent,
October 1st, 1859.

ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

BY CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

The right of Translation is reserved.

The Origin laid out the central tenants of Darwin's theory

1. **Variation exists among individuals**

2. **Some variants are more successful than others**

3. **Variation is heritable**

The critical contribution being a mechanism for evolution: Natural selection

Using life tables: A practice question

A team of conservation biologists is interested in determining the optimum environment for raising an endangered species of flowering plant in captivity. For their purposes, the optimum environment is the one that maximizes the growth rate of the captive population allowing more individuals to be released into the wild in each generation. To this end, they estimated life table data for two cohorts (each of size 100) of captive plants, each raised under a different set of environmental conditions. Using the data in the hypothetical life tables below, answer the following questions:

Population 1
(in environment 1)

x	N_x	l_x	m_x
1	100	1.0	0
2	50	.50	0
3	25	.25	8
4	10	.10	10

Population 2
(in environment 2)

x	N_x	l_x	m_x
1	100	1.0	2
2	50	.50	2
3	25	.25	0
4	10	.10	0

A. Using the data from the hypothetical life tables above, calculate the expected number of offspring produced by each individual plant over its life, R_0, for each of the populations.

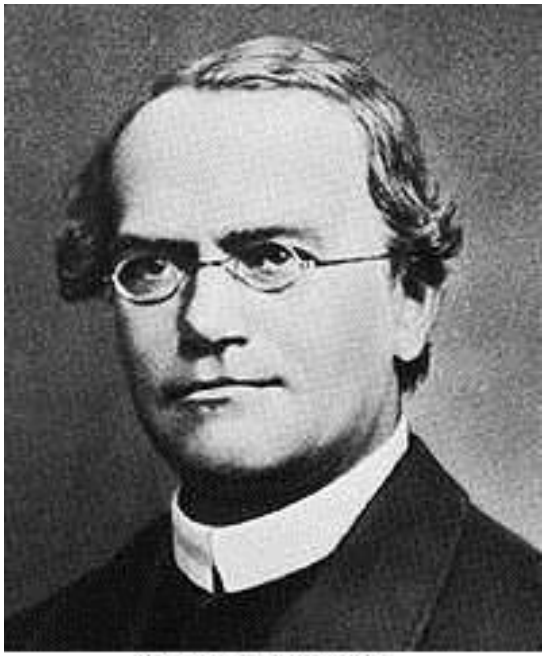
B. Using the data in the life tables above, calculate the generation time for each of the populations.

C. Using your calculations in A and B, estimate the population growth rate, *r*, of the two populations. Which population is growing faster? Why?

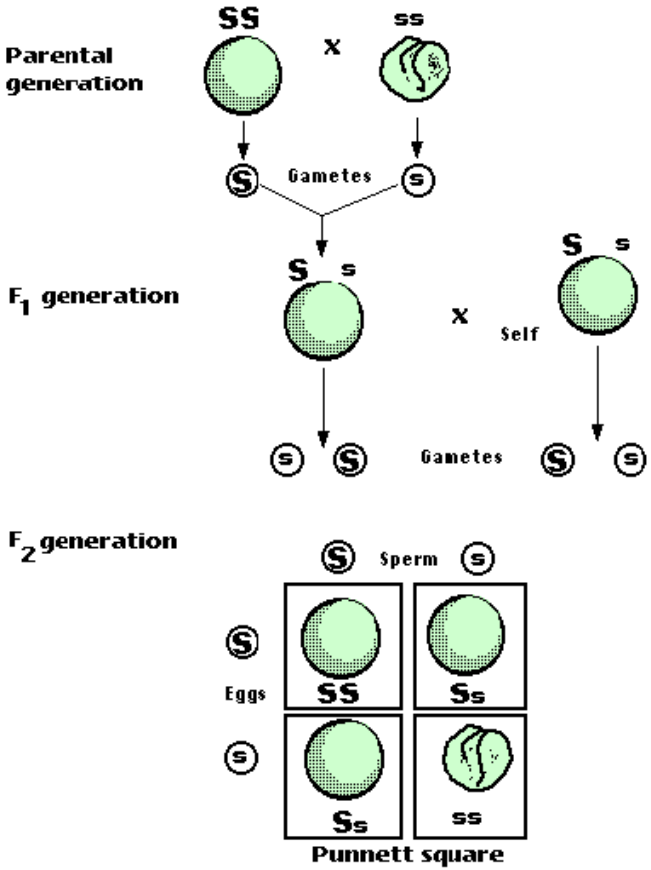
D. Assuming the populations both initially contain 100 individuals, estimate the size of each population in five years.

E. If the sole goal of the conservation biologists is to maximize the growth rate of the captive population, which conditions (those experienced by population 1 or 2) should they use for their future programs?

Darwin had elucidated the driving force of evolution but the problem of inheritance persisted until 1900 when Gregor Mendel's work was rediscovered



Gregor Mendel



Mendel's results showed that inheritance was 'particulate' not 'blending'

In conjunction with a fundamental mathematical result, Mendel's work showed how variation is maintained

G.H. Hardy

<u>Hardy-Weinberg equilibrium</u>

$$p^2 + 2pq + q^2 = 1$$

Undoubtedly you have seen this result before, but:

- **What does it actually mean?**
- **Where does it come from?**
- **Why was it historically important?**

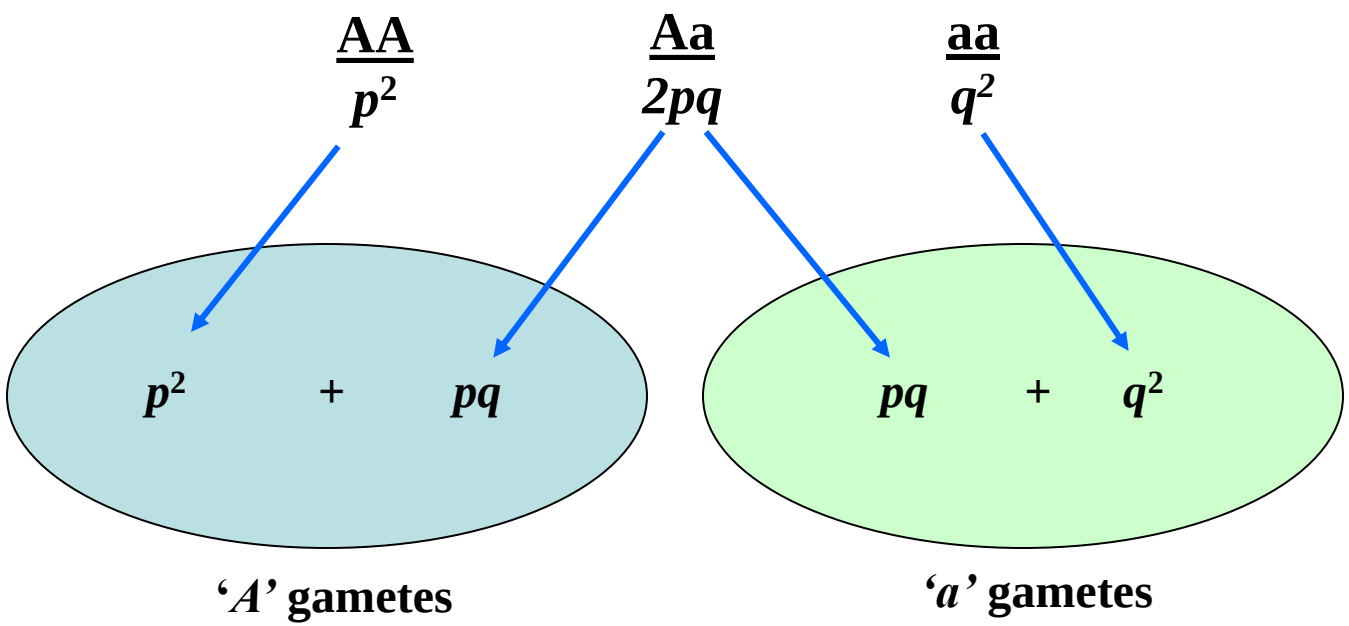
Where does this result come from?

Imagine a parental population with the following genotypes and frequencies:

Genotype	AA	Aa	aa
Frequency	p^2	$2pq$	q^2

- ***p*** **is the frequency of the '*A*' allele**
- ***q*** **is the frequency of the '*a*' allele and = 1-*p***

These parental genotypes contribute to the gamete pool as follows:



Where does this equation come from?

$$\boxed{p^2 + pq} = p^2 + p(1-p) = p^2 + p - p^2 = p$$

From previous slide

'*A*' gametes

$$\boxed{pq + q^2} = (1-q)q + q^2 = q - q^2 + q^2 = q$$

From previous slide

'*a*' gametes

If the next parental generation is formed by the random union of these gametes

What is the probability of generating '*AA*' parents? $= p*p = p^2$

What is the probability of generating '*Aa*' parents? $= p*q + q*p = 2pq$

What is the probability of generating '*aa*' parents? $= q*q = q^2$

These genotype frequencies are exactly those we started with!

This demonstrates that with random mating and particulate inheritance, genetic variation is maintained forever – the critical historical contribution of Hardy-Weinberg

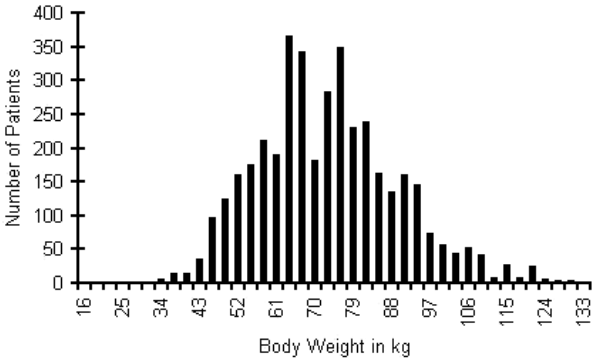
What are the assumptions of the Hardy-Weinberg equilibrium?

- **Random mating**
- **No selection**
- **Infinitely large population**
- **No gene flow**
- **No mutation**

If any of these assumptions are violated evolution occurs

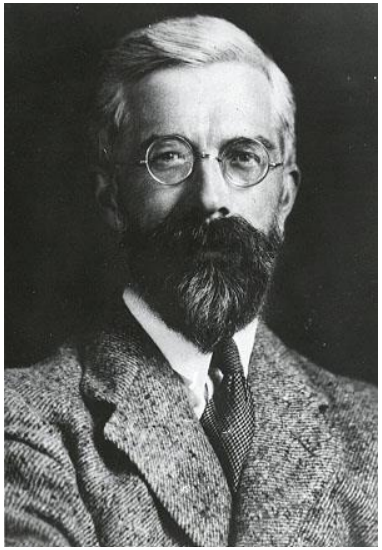
The discovery that inheritance is particulate led to a new debate

Biometricians – Evolution proceeds by acting on what is more or less continuous variation. This was Darwin's view and was championed by his cousin Francis Galton.



Mendelians – Emphasized discrete variation and new mutations. De-emphasized continuous variation and the role of natural selection.

The modern synthesis (1930-1950)



R.A. Fisher
(1890-1962)

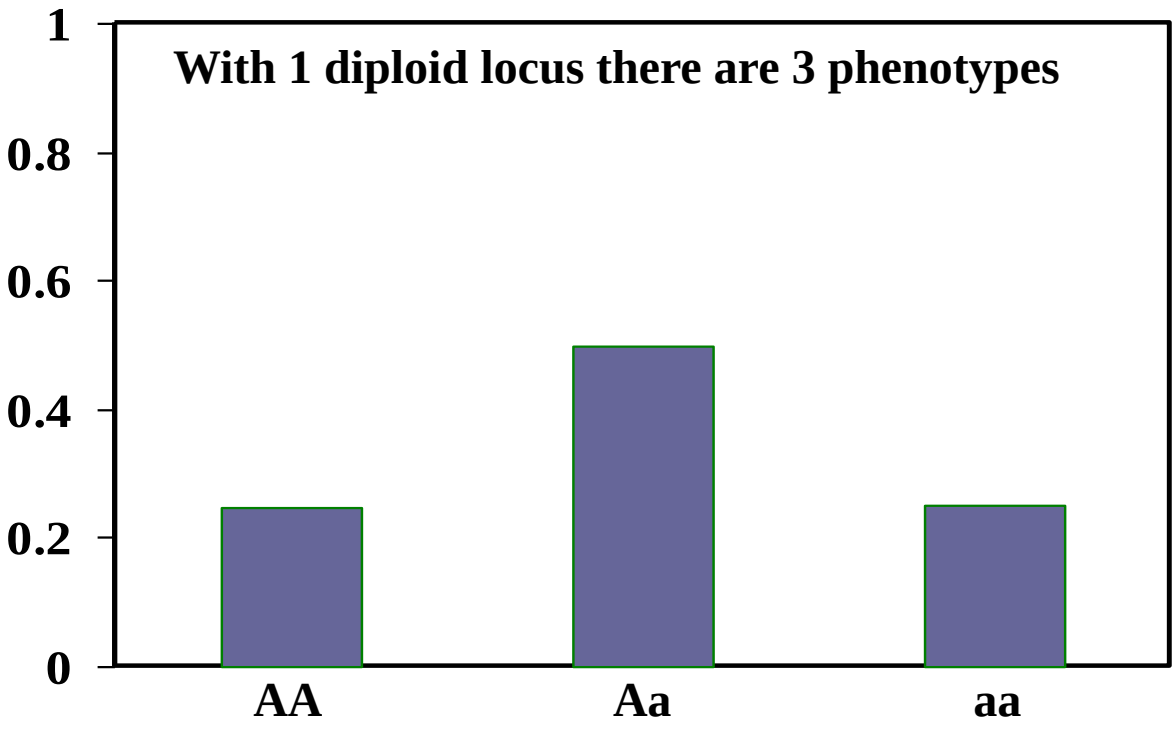
S. Wright
(1889-1988)

J.B.S. Haldane
(1892-1964)

Used mathematics to resolve the debate over the nature of genetic variation

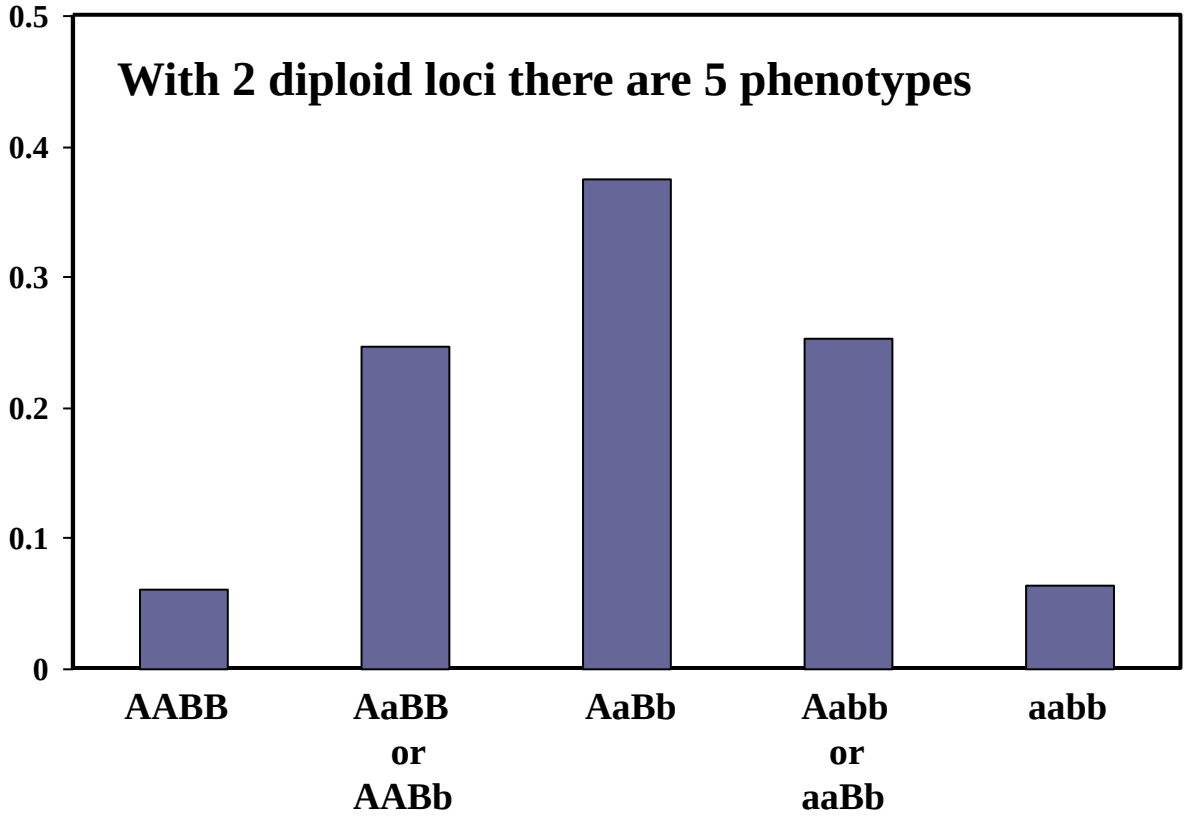
Synthesizing the nature of variation

Imagine a case where an individual's phenotype is equal to the number of "capital" alleles in its genome

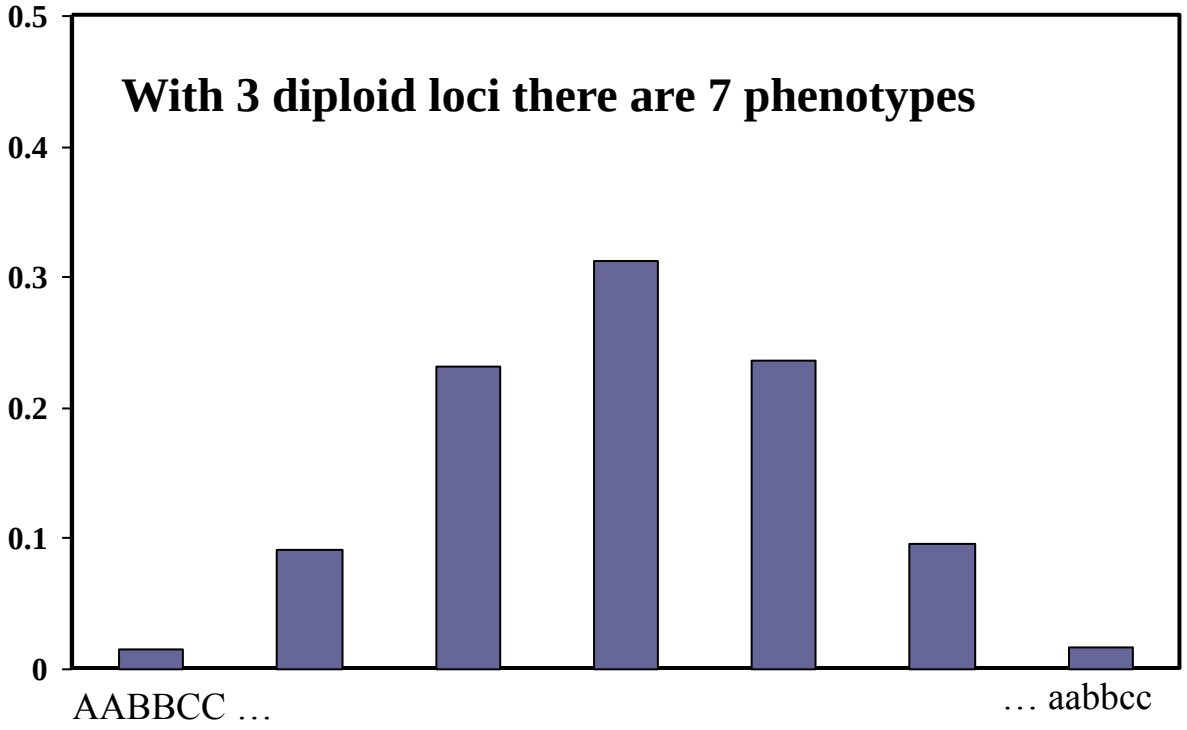


Variation is quite discrete!

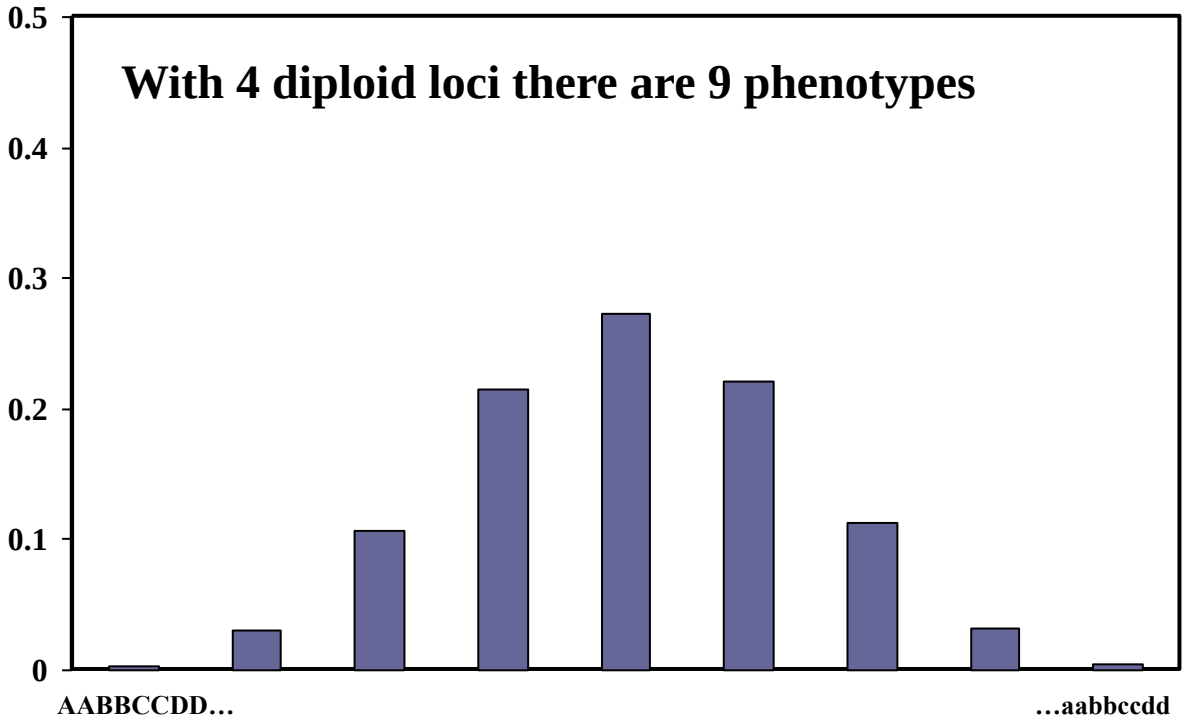
Synthesizing the nature of variation



Synthesizing the nature of variation



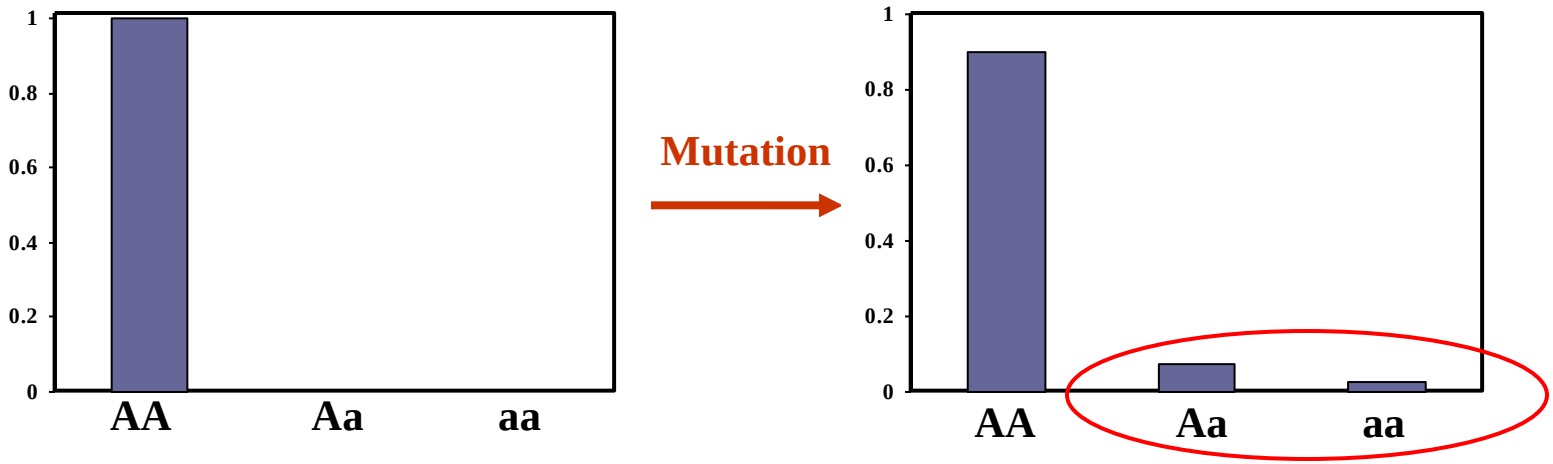
Synthesizing the nature of variation



Conclusion: Particulate inheritance can generate continuous variation

Synthesizing the role of mutation and selection in evolution

- Mutation generates new genetic variation



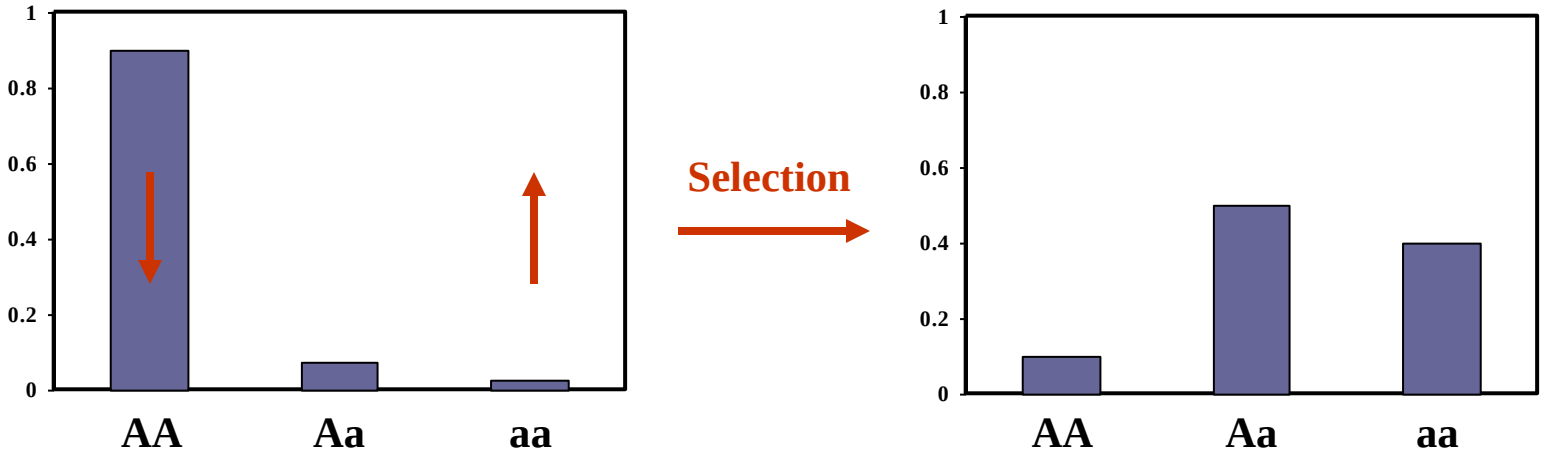
No genetic variation

Genetic variation

- The genetic variation generated by mutation is RANDOM with respect to fitness

Synthesizing the role of mutation and selection in evolution

- **The RANDOM variation produced by new mutations is the raw material for selection**



In summary…

<u>Darwin showed that:</u>

1. **Variation exists between individuals**

2. **Some variants are more successful than others**

3. **Variation is heritable (but how?)**

<u>Eventually the missing pieces were filled in:</u>

1. Inheritance is particulate and thus genetic variation does not dilute over time (Mendel, Hardy-Weinberg)

2. Particulate inheritance can readily generate continuous distributions

3. RANDOM mutation is the ultimate source of variation upon which natural selection acts

Assessing genetic variation and Hardy-Weinberg I: a practice problem

The scenario: A group of biologists was studying a population of elk in an effort to quantify genetic variation at disease resistance locus. Through DNA sequencing, the biologists have determined that there are two alleles at this locus, **A** and **a**. Sequencing analysis of many individuals has also allowed the frequency of the alleles and the corresponding diploid genotypes to be estimated

The data:
Frequency of the **A** allele is $p = 0.4$
Frequency of the **a** allele is $q = ?$

Frequency of the **AA** genotype is: 0.06
Frequency of the **Aa** genotype is: 0.80
Frequency of the **aa** genotype is: 0.14

The question:
Is this population in Hardy-Weinberg Equilibrium? Justify your response.

Assessing genetic variation and Hardy-Weinberg II: a practice problem

The scenario: A group of biologists was studying a population of flowers where flower color is controlled by a single diploid locus with two alleles. Individuals with genotype **AA** make white flowers, individuals with genotype **Aa** make red flowers, and individuals with genotype **aa** make red flowers.

The data:
Frequency of the white flowers is *f(white)* = 0.4
Frequency of red flowers is f(red) = ?

The questions:

1. Which allele, **A** or **a** is dominant?

2. Assuming that this population is in Hardy-Weinberg Equilibrium, what is the frequency of the **A** allele?

3. Assuming that this population is in Hardy-Weinberg Equilibrium, what is the frequency of the **a** allele?