浙江大学
生命演化研究中心

The introduction of Standard Evolutionary Theory (SET) --Modern Synthesis

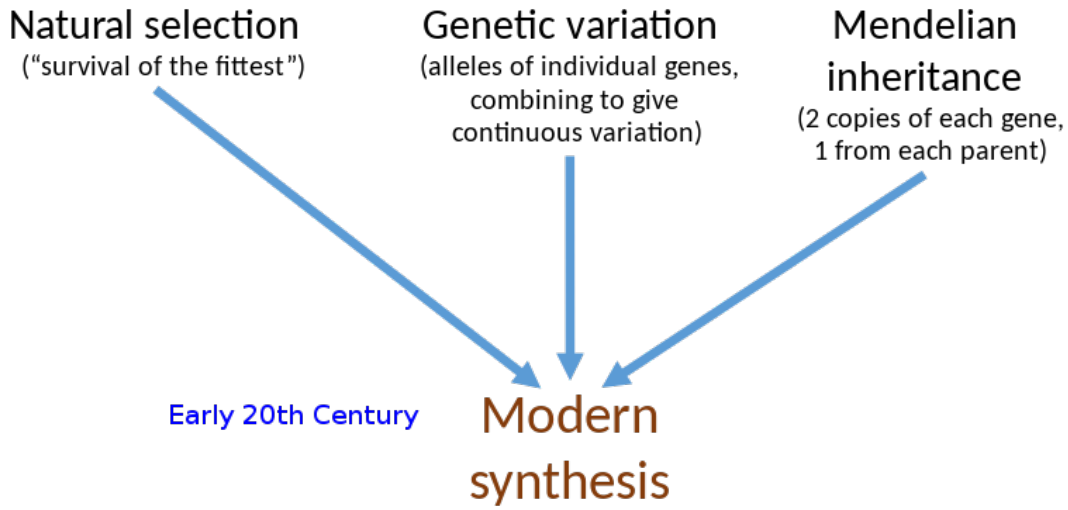
卢妍林 & 陈光霁

2022年9月17日

- **Background**

Standard evolutionary theory, SET

*"Standard evolutionary theory is **gene-centered**, and treats as evolutionary processes solely those events that change gene frequencies"*



主要因素：

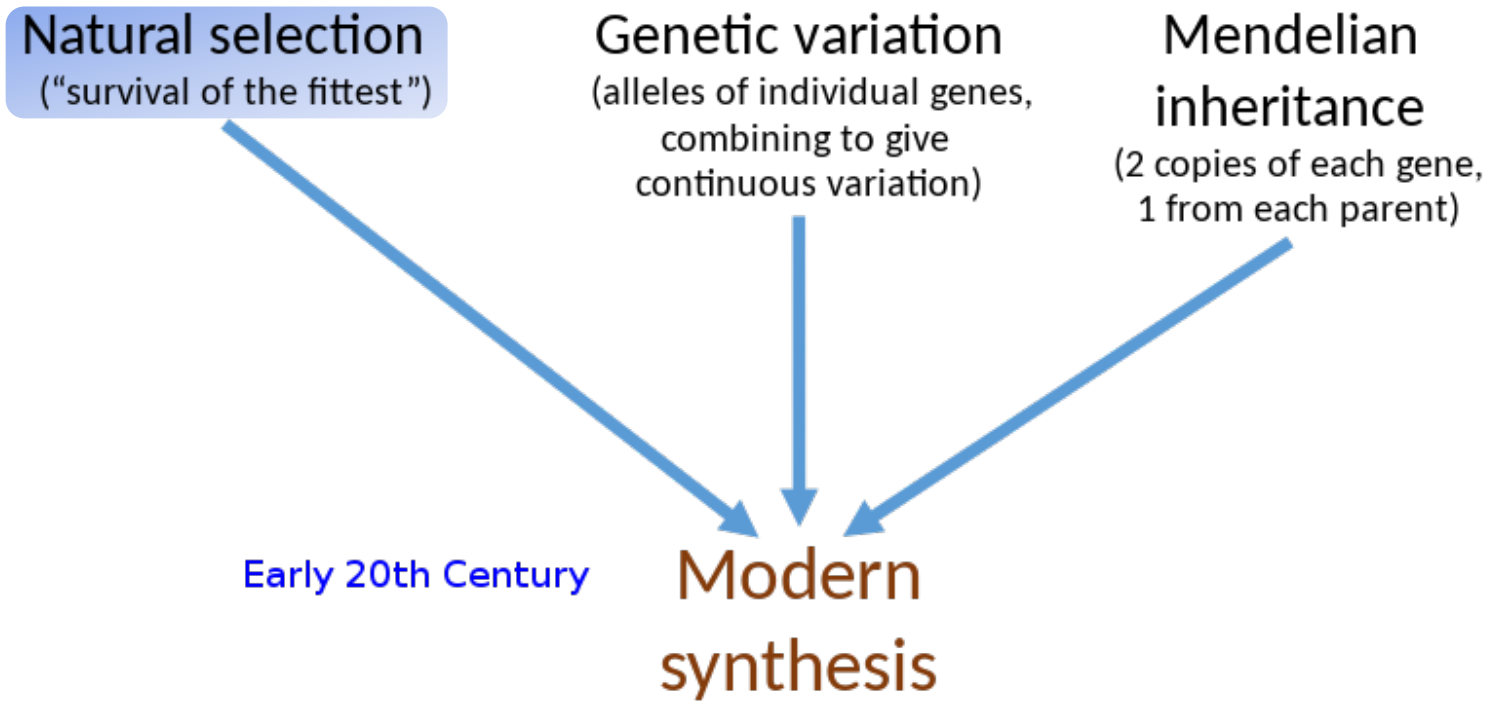
1.Mutation: *introduces new variants at random. Repeated occurrence of the same genetic variants is called mutation pressure.*

2.Natural selection: *makes adaptive variants more common through differential survival and reproduction.*

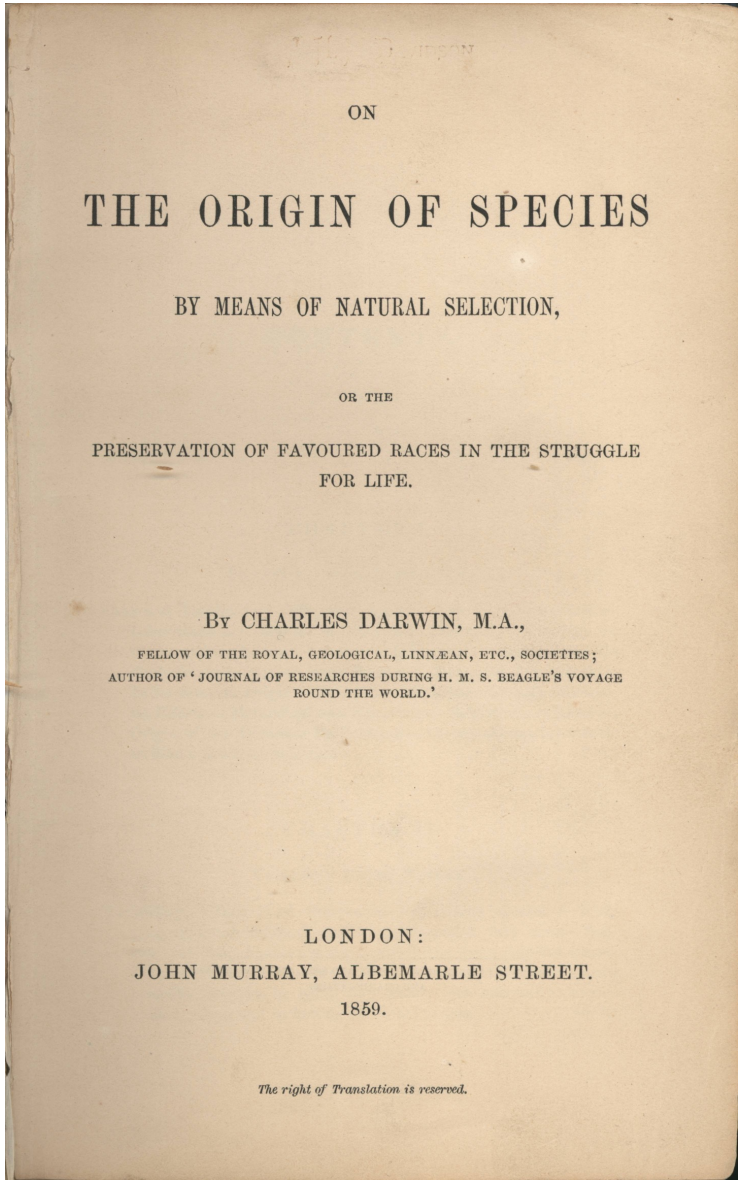
3.Genetic drift: *random changes in frequency of genetic variants due to sampling.*

4.Gene flow: *variants enter and leave a population via migration, dispersal or mating.*

- **Background**


Natural selection
("survival of the fittest")
Genetic variation
(alleles of individual genes, combining to give continuous variation)
Mendelian inheritance
(2 copies of each gene, 1 from each parent)
Early 20th Century
Modern synthesis

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.

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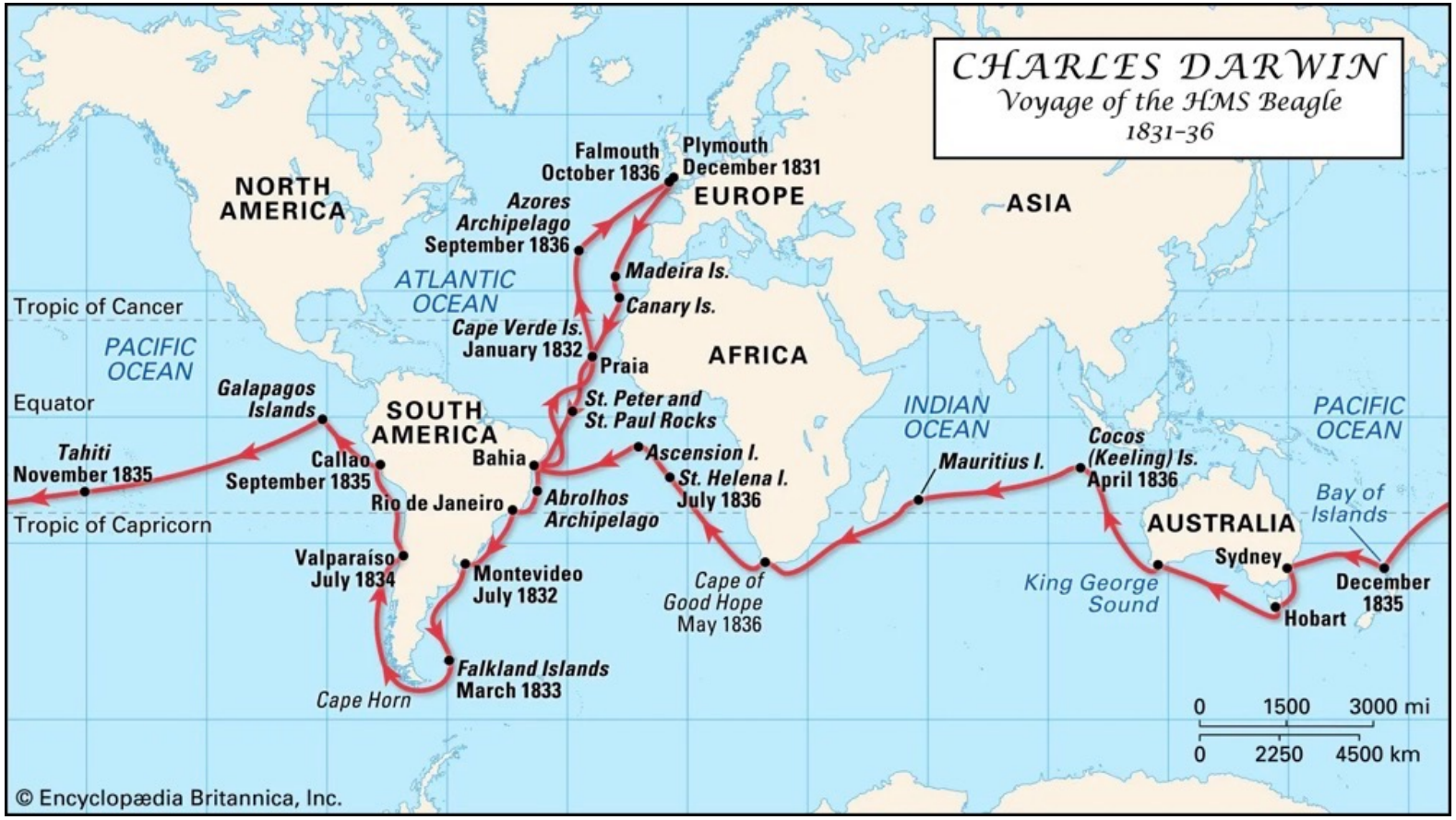
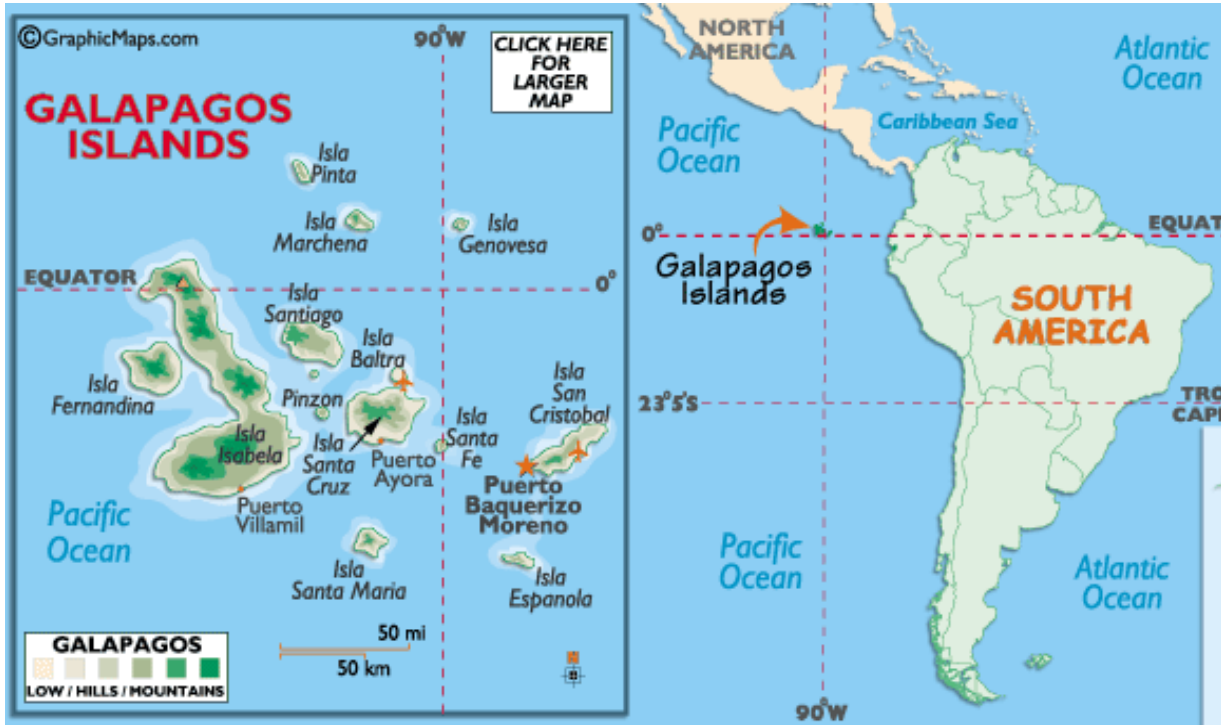
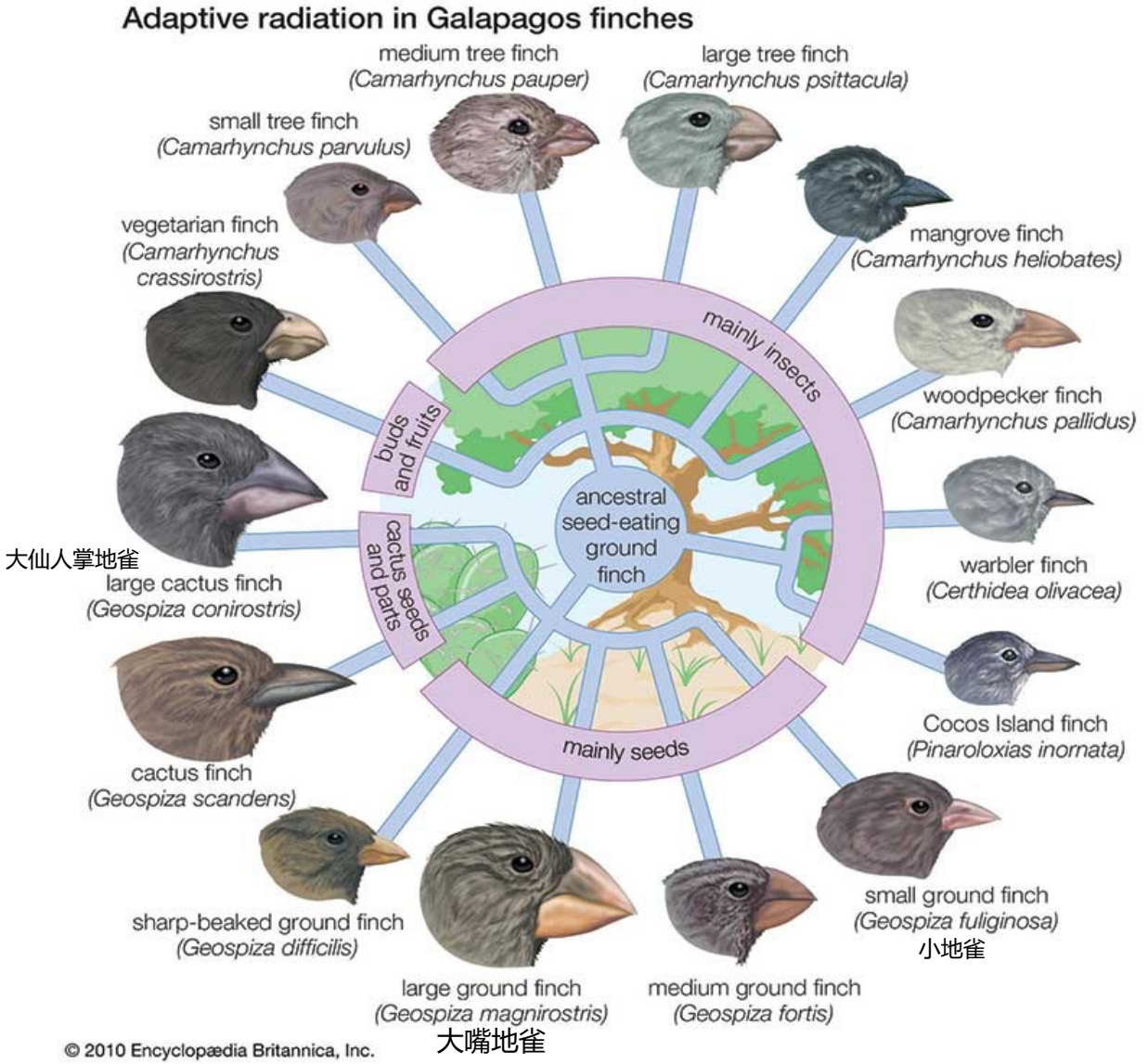
物种起源

《论依据自然选择即在生存斗争中保存优良族的物种起源》



1859


©GraphicMaps.com
90°W
CLICK HERE FOR LARGER MAP
GALAPAGOS ISLANDS
Isla Pinta
Isla Marchena
Isla Genovesa
EQUATOR
0°
Isla Santiago
Isla Baltra
Isla Fernandina
Pinzon
Isla San Cristobal
Isla Isabela
Isla Santa Cruz
Puerto Ayora
Isla Santa Fe
Puerto Villamil
Puerto Baquerizo Moreno
Pacific Ocean
Isla Santa Maria
Isla Espanola
GALAPAGOS
LOW / HILLS / MOUNTAINS
50 mi
50 km
NORTH AMERICA
Atlantic Ocean
Caribbean Sea
Pacific Ocean
0°
Galapagos Islands
EQUAT
SOUTH AMERICA
23°5'S
TRO CAP
Pacific Ocean
Atlantic Ocean
90°W


Adaptive radiation in Galapagos finches
medium tree finch (Camarhynchus pauper)
large tree finch (Camarhynchus psittacula)
small tree finch (Camarhynchus parvulus)
mangrove finch (Camarhynchus heliobates)
vegetarian finch (Camarhynchus crassirostris)
woodpecker finch (Camarhynchus pallidus)
mainly insects
buds and fruits
ancestral seed-eating ground finch
cactus seeds and parts
warbler finch (Certhidea olivacea)
大仙人掌地雀
large cactus finch (Geospiza conirostris)
Cocos Island finch (Pinaroloxias inornata)
mainly seeds
cactus finch (Geospiza scandens)
small ground finch (Geospiza fuliginosa)
小地雀
sharp-beaked ground finch (Geospiza difficilis)
large ground finch (Geospiza magnirostris)
大嘴地雀
medium ground finch (Geospiza fortis)
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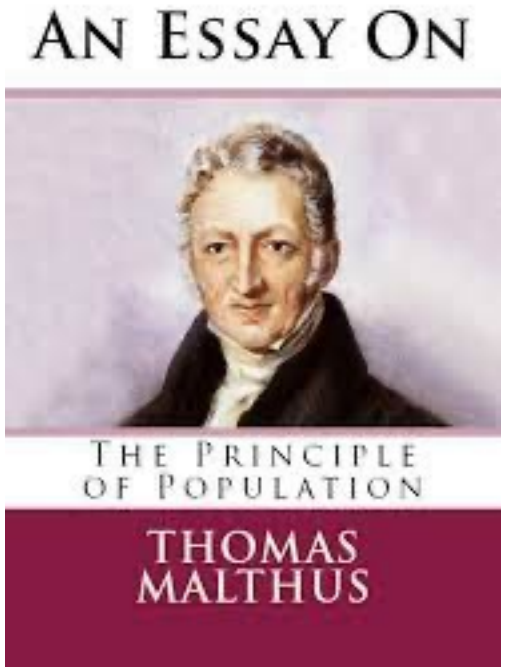
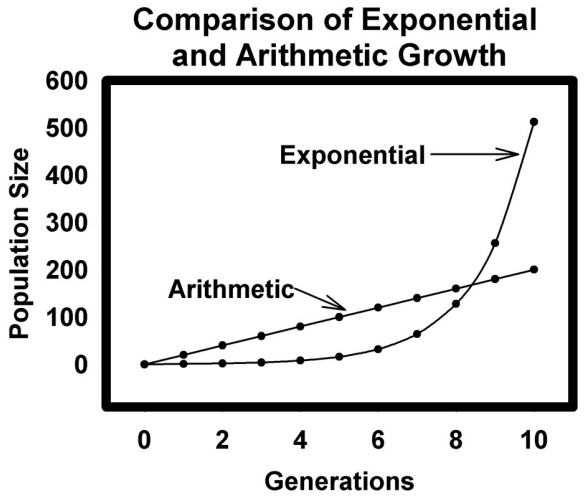
适应环境

- **人口论**

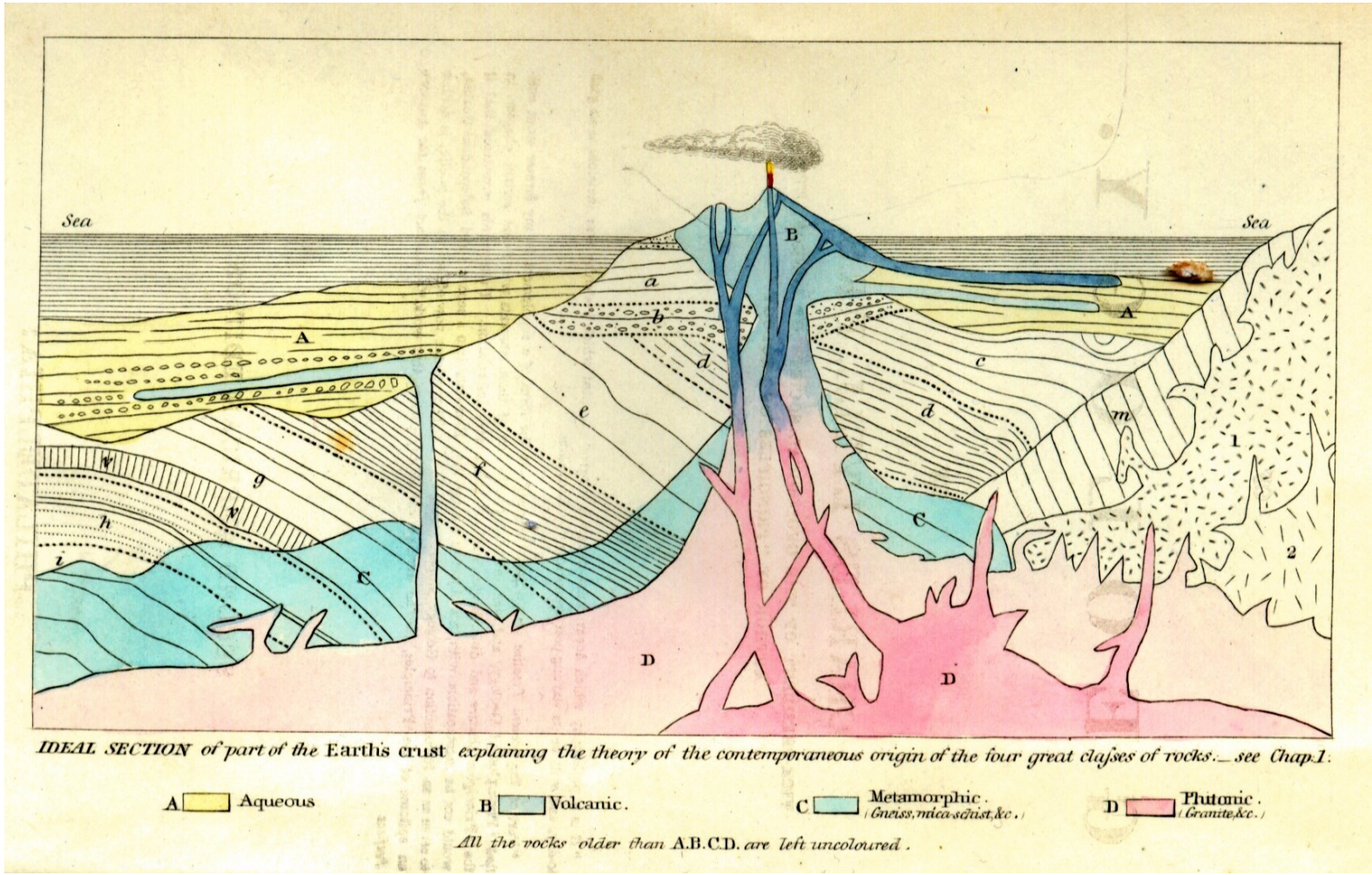


1798



- 人类粮食的生产永远无法赶上人口的增加，致使粮食供不应求，进而发生饥荒或战争，导致一部分人口死亡。

- **地质学原理**



Principles of Geology

- 地球的地形、地貌是经过了长时间细微改造的结果；
- 风、雨、冰雪等微小的力量，持续千万年后就可以改变地表的形貌。

Lyell used the theory of uniformitarianism to describe how the Earth's surface was changing over time.

- **自然选择学说的解释模型**

事实1：生物都有过度繁殖的倾向

事实2：物种内的个体数能保持稳定

事实3：资源是有限的

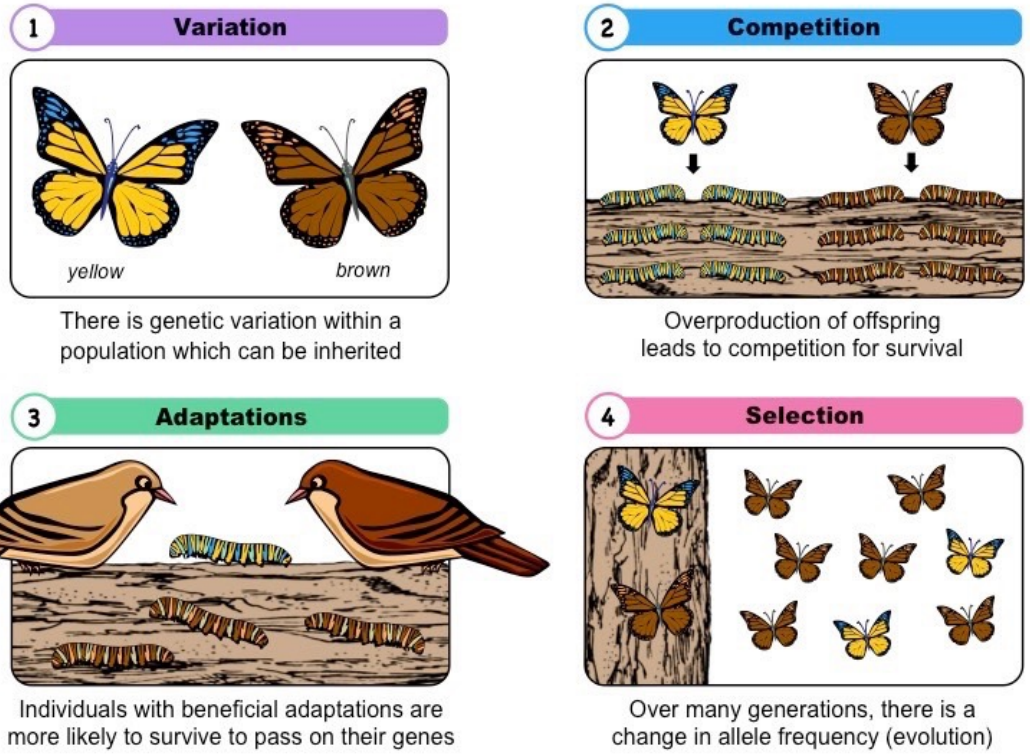
推论1：个体间存在着生存斗争

事实4：个体间普遍存在差异（变异）

事实5：许多变异是可以遗传的

推论2：具有有利变异的个体，生存并留下后代的机会更多

推论3：有利变异逐代积累，生物不断演化出新类型



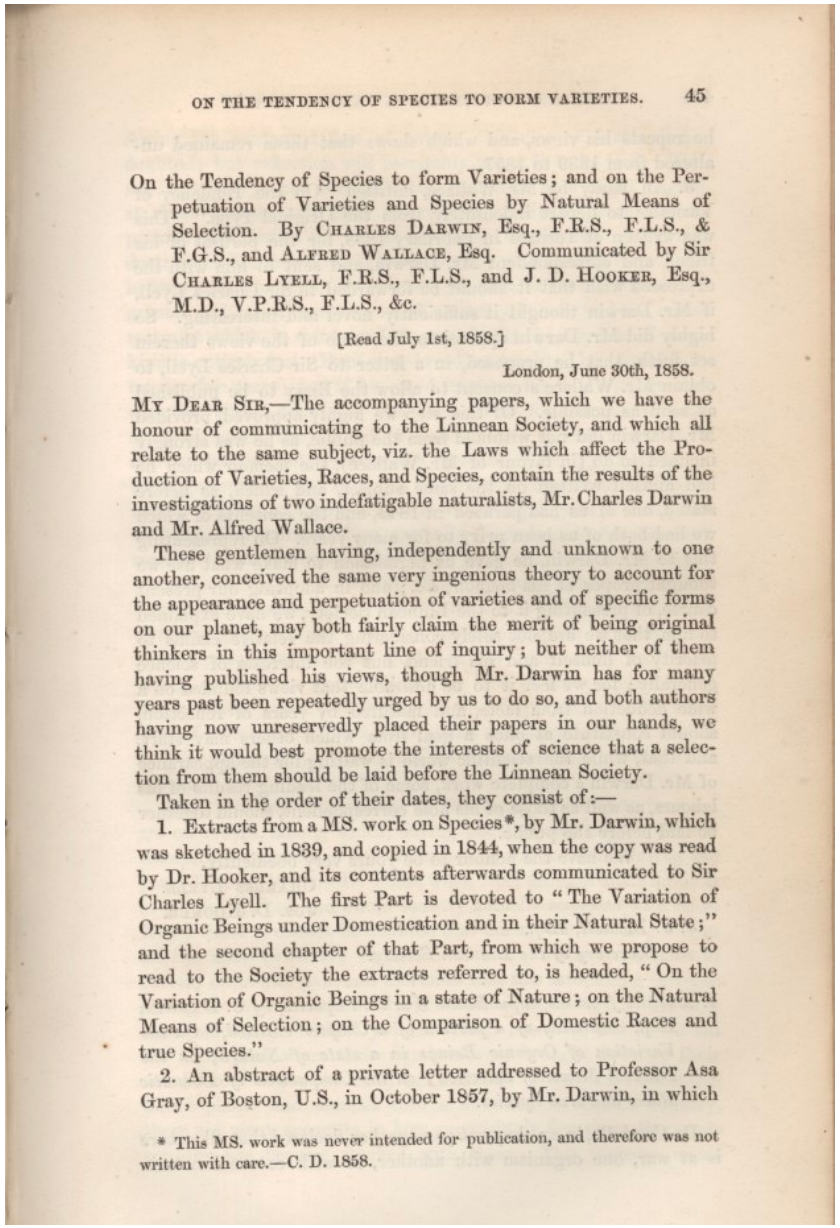
1.过度繁殖

2.生存斗争

3.遗传和变异

4.适者生存

- 1858



ON THE TENDENCY OF SPECIES TO FORM VARIETIES. 45

On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection. By CHARLES DARWIN, Esq., F.R.S., F.L.S., & F.G.S., and ALFRED WALLACE, Esq. Communicated by Sir CHARLES LYELL, F.R.S., F.L.S., and J. D. HOOKER, Esq., M.D., V.P.R.S., F.L.S., &c.

[Read July 1st, 1858.]

London, June 30th, 1858.

MY DEAR SIR,—The accompanying papers, which we have the honour of communicating to the Linnean Society, and which all relate to the same subject, viz. the Laws which affect the Production of Varieties, Races, and Species, contain the results of the investigations of two indefatigable naturalists, Mr. Charles Darwin and Mr. Alfred Wallace.

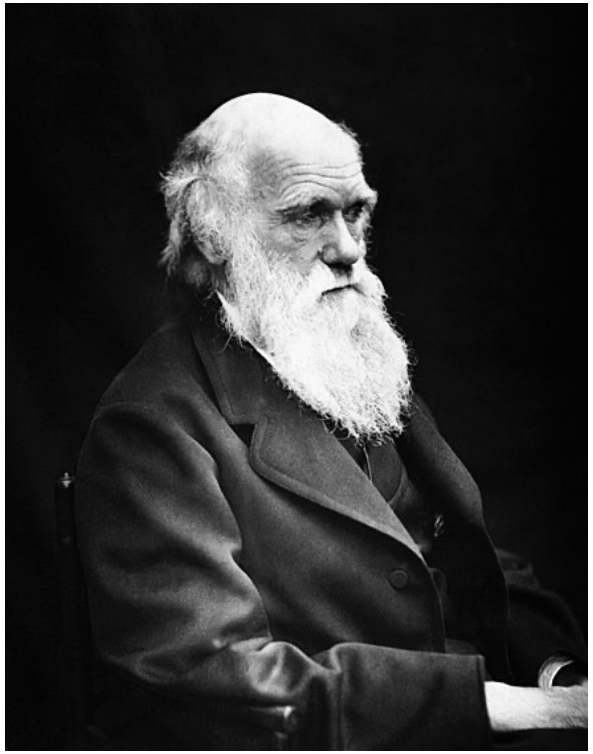
These gentlemen having, independently and unknown to one another, conceived the same very ingenious theory to account for the appearance and perpetuation of varieties and of specific forms on our planet, may both fairly claim the merit of being original thinkers in this important line of inquiry; but neither of them having published his views, though Mr. Darwin has for many years past been repeatedly urged by us to do so, and both authors having now unreservedly placed their papers in our hands, we think it would best promote the interests of science that a selection from them should be laid before the Linnean Society.

Taken in the order of their dates, they consist of:—

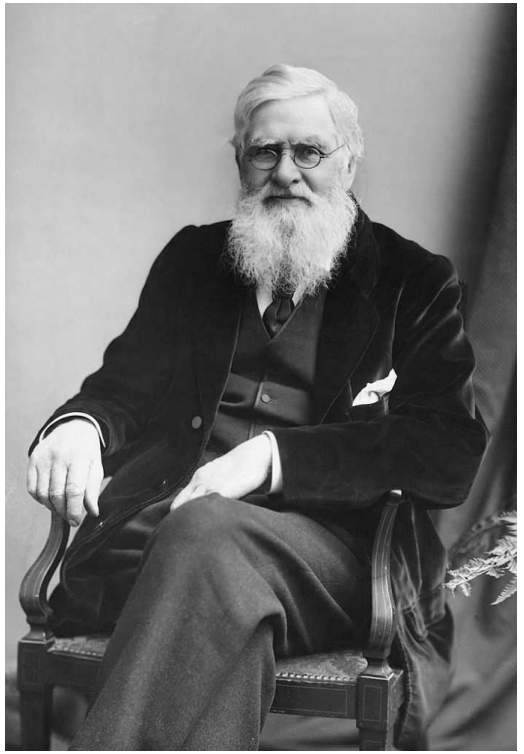
1. Extracts from a MS. work on Species*, by Mr. Darwin, which was sketched in 1839, and copied in 1844, when the copy was read by Dr. Hooker, and its contents afterwards communicated to Sir Charles Lyell. The first Part is devoted to "The Variation of Organic Beings under Domestication and in their Natural State;" and the second chapter of that Part, from which we propose to read to the Society the extracts referred to, is headed, "On the Variation of Organic Beings in a state of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and true Species."

2. An abstract of a private letter addressed to Professor Asa Gray, of Boston, U.S., in October 1857, by Mr. Darwin, in which

* This MS. work was never intended for publication, and therefore was not written with care.—C. D. 1858.



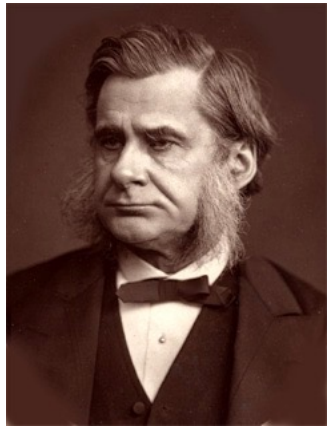
Charles Robert Darwin
(1809-1882)



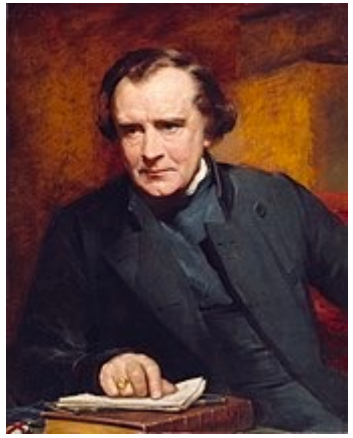
Alfred Russel Wallace
(1823-1913)

1858年7月1日，伦敦林奈学会发布了由达尔文和华莱士共同署名的关于自然选择的论文

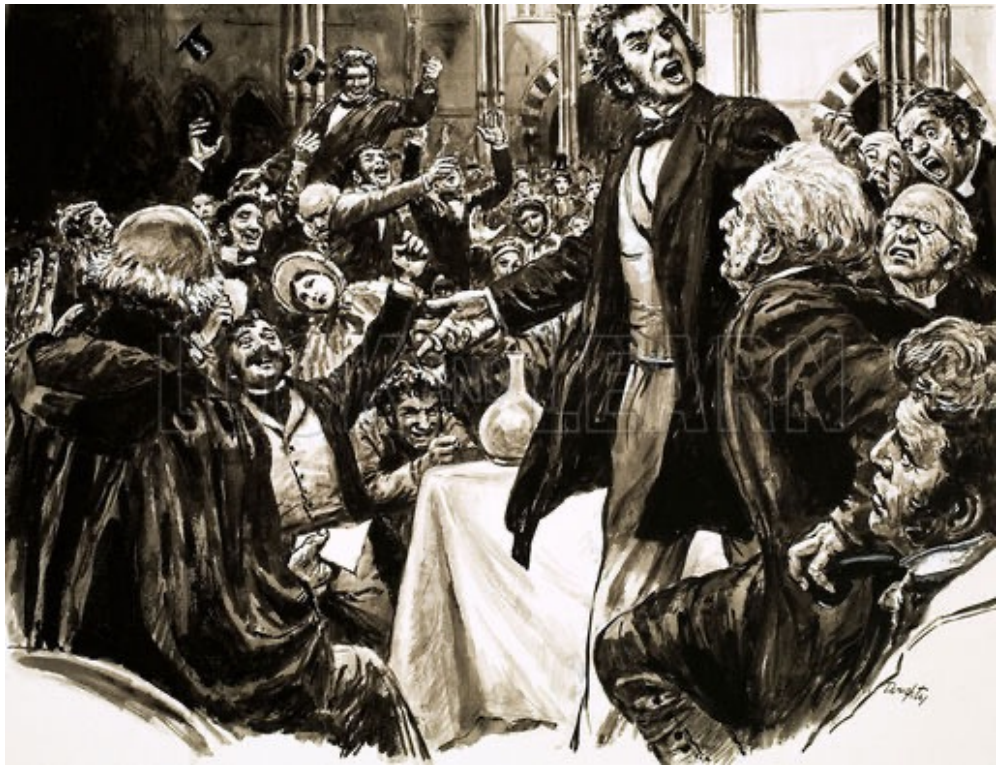
Oxford Evolution Debate



Thomas Henry Huxley
(1825-1895)

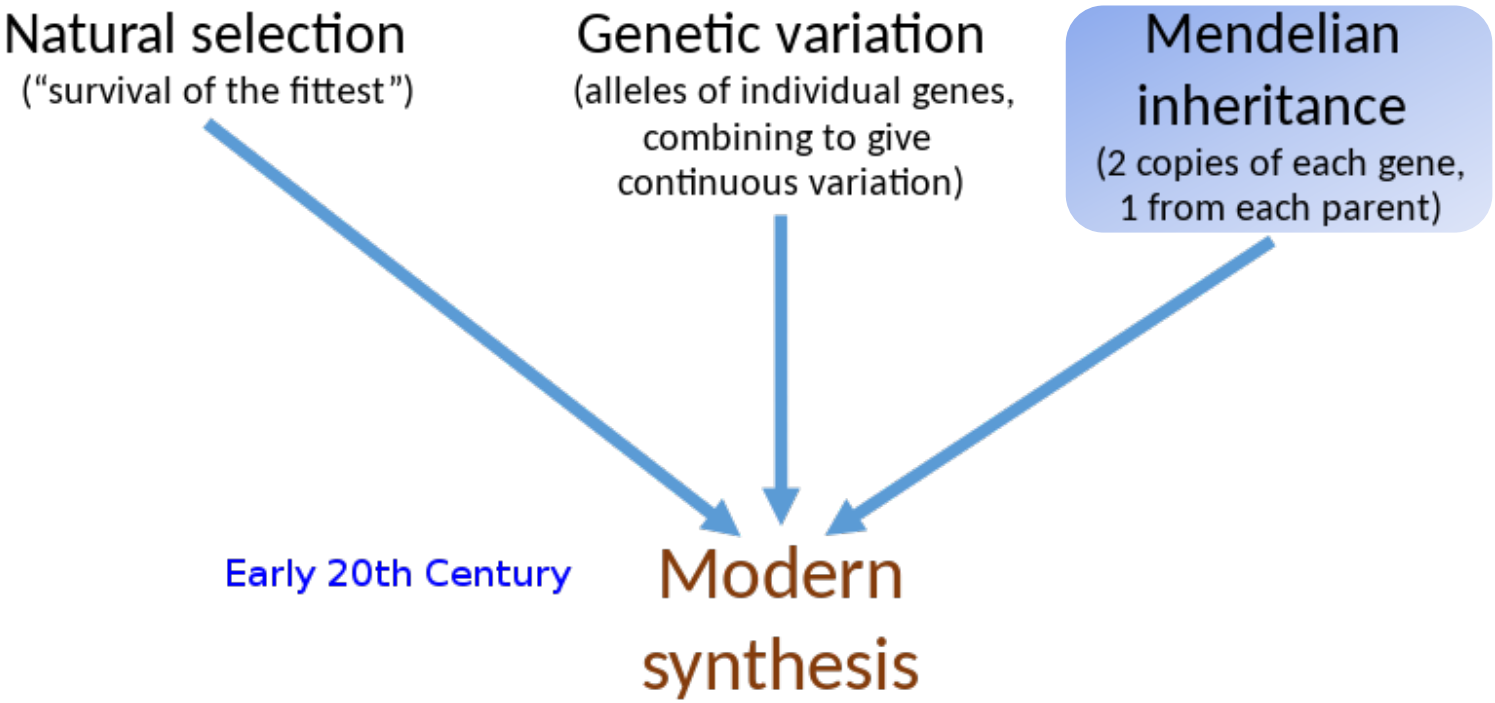


Samuel Wilberforce
(1805-1873)



- Proponents and opponents of Darwin & Wallace's theories clash in the famous Oxford Evolution Debate;
- Thomas Henry Huxley and Samuel Wilberforce butt heads in a public debate, which both sides consider a victory.

- **Background**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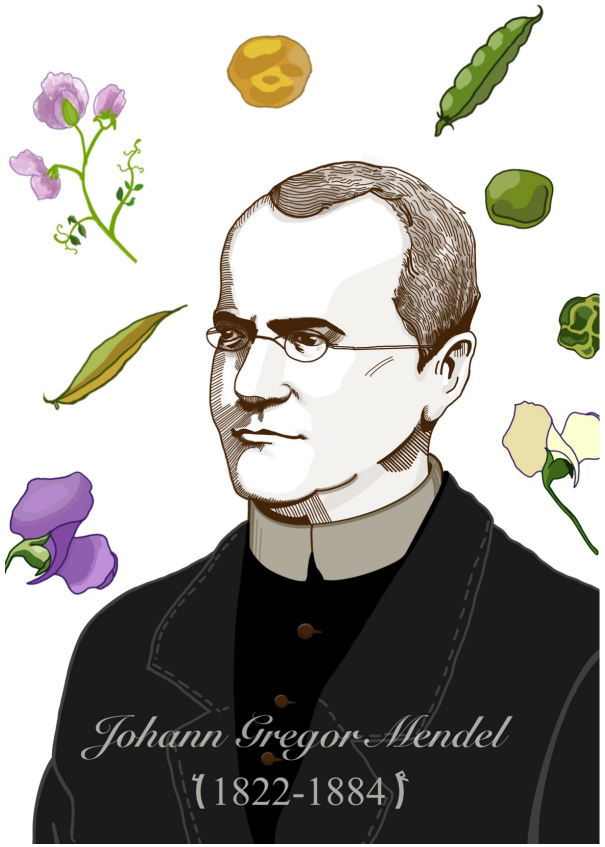
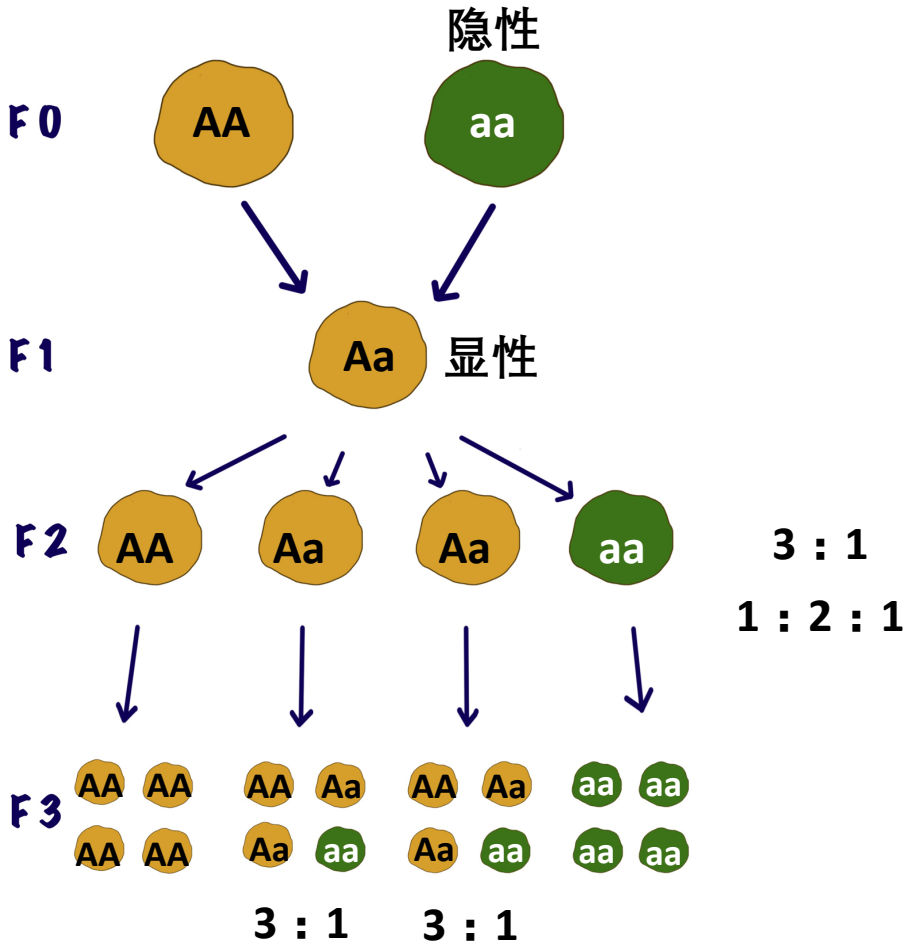


Experiments on plant hybridization



Pisum(豌豆)

1.自花授粉

2.异花授粉

3.较易人为控制

- 显性 vs 隐性
- 分离律
- 自由组合律
- 遗传因子、数学模型……

-- 素材来源于饶毅老师的“孤独的天才”

entsprechen den Hybriden A_1a und A_2a die Entwicklungsreihen

$$A_1 + 2A_1a + a.$$
$$A_2 + 2A_2a + a.$$

Die Glieder dieser Reihen können in 9 verschiedenen Kombinationen auftreten und jede derselben stellt die Zusammensetzung für eine bestimmte Zahl vor:

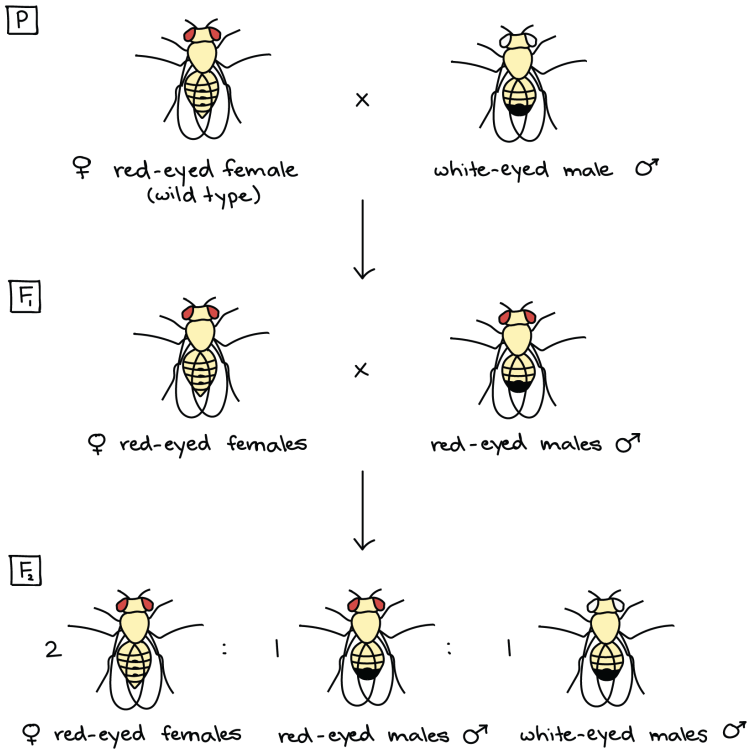
1	A_1	A_2	2	A_1a	A_2	1	A_2	a
2	A_1	A_2a	4	A_1a	A_2a	2	A_2a	a
1	A_1	a	2	A_1a	a	1	a	a

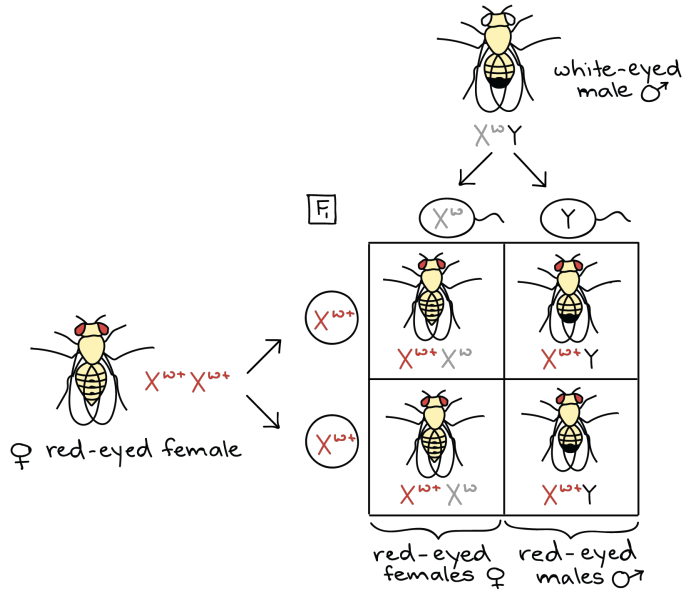
Die den einzelnen Kombinationen vorausgesetzten Zahlen geben zugleich an, wie viele Pflanzen mit den entsprechenden Gliedern in die Reihe gehören. Da die Summe derselben 16 beträgt, so sind künftig Zahlen im Durchschnitte auf je 16 Pflanzen zu setzen, jedoch wird die Reihe selbst zeigen in wieweit Abweichungen.

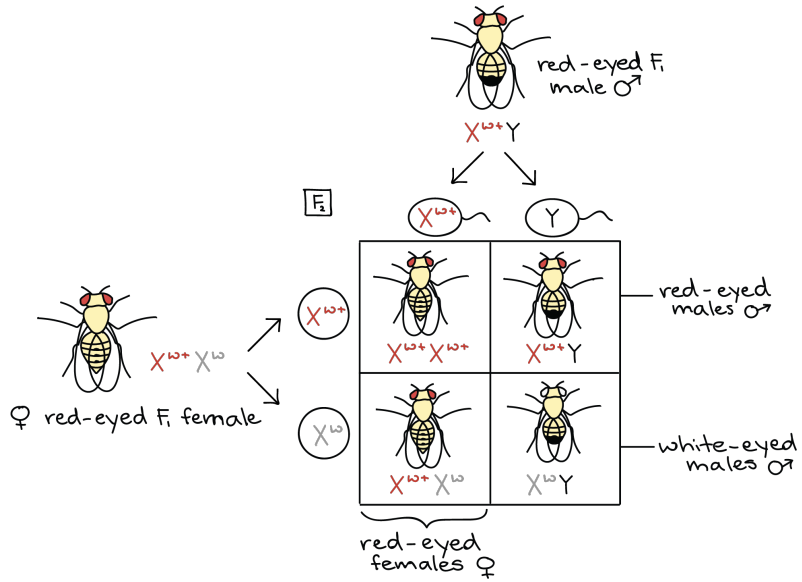
-- 孟德尔关于遗传因子的手稿

1859 1860 1866 1910

Thomas Hunt Morgan
(1866-1945)
1933年获得了诺贝尔生理医学奖

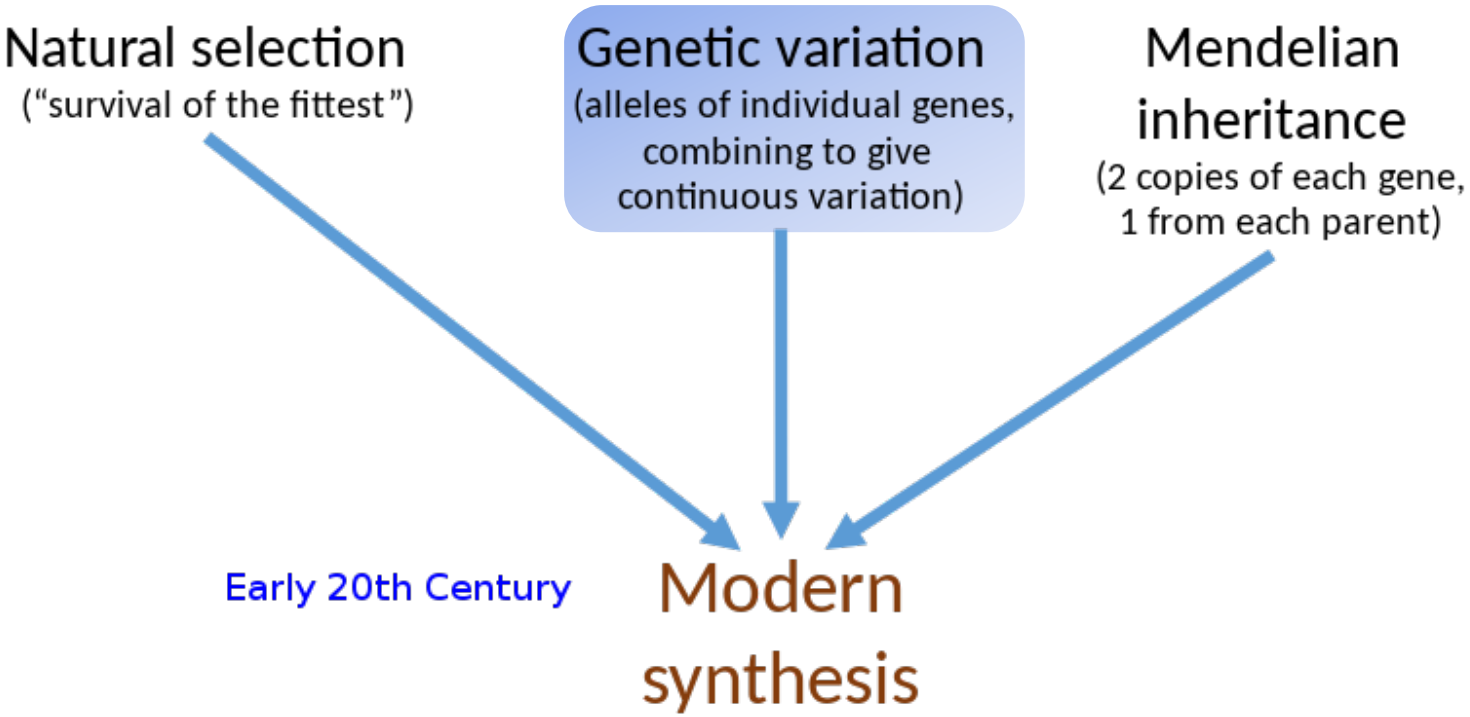






https://www.khanacademy.org/science/ap-biology/heredity/chromosomal-inheritance-ap/a/discovery-of-the-chromosomal-basis-of-inheritance

- **Background**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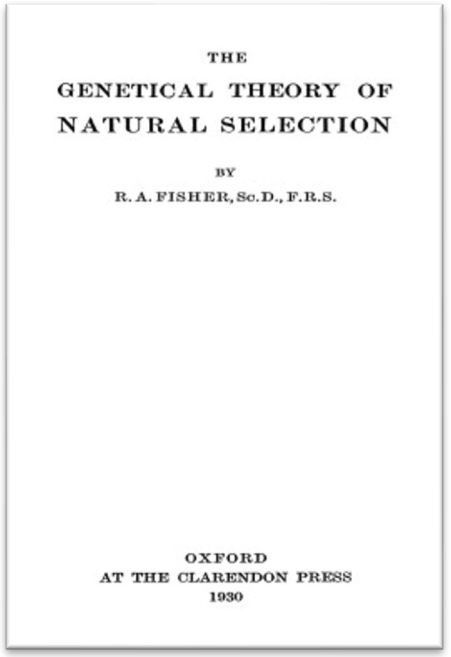
Modern synthesis

1859 1860 1866 1910 1930

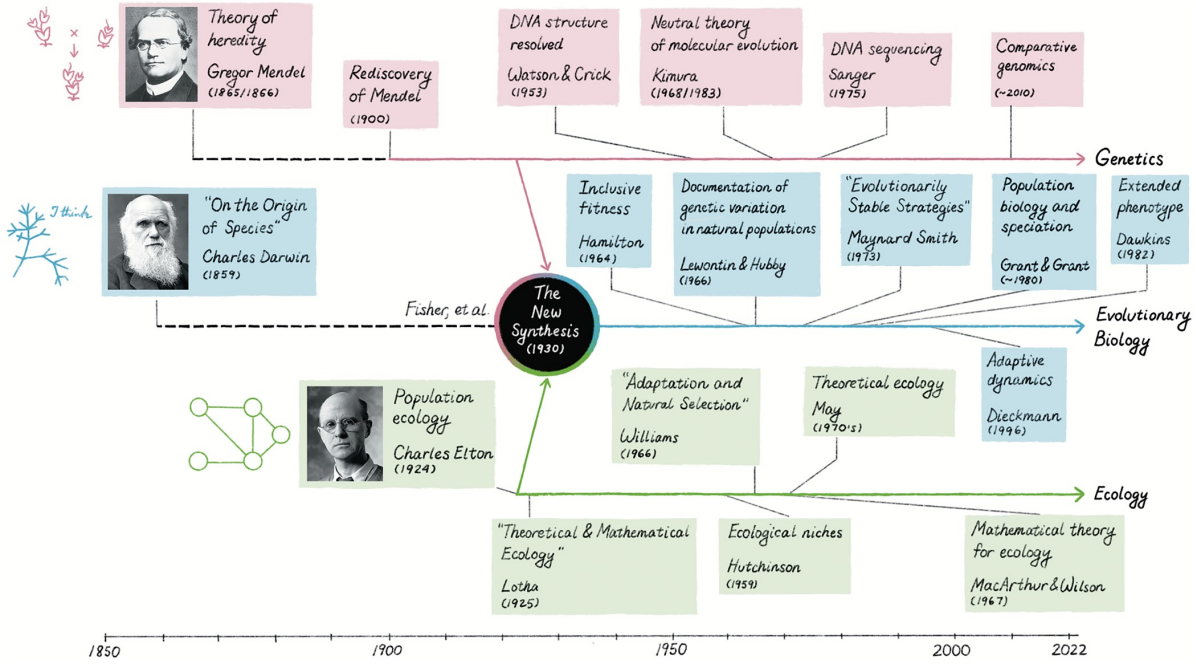
Ronald Fisher
(1890-1962)

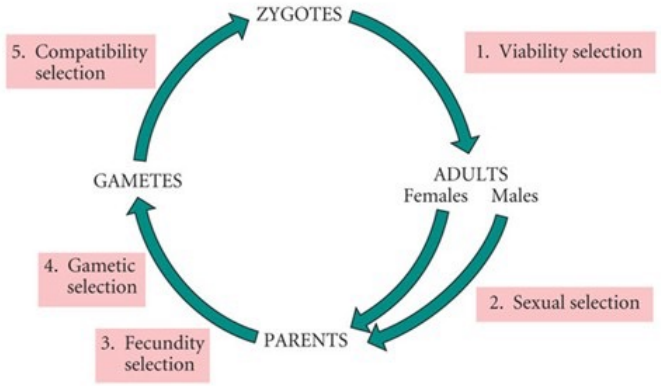


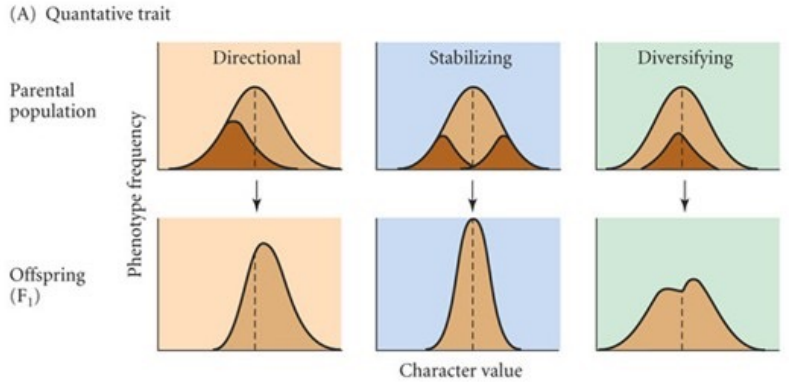
THE
GENETICAL THEORY OF
NATURAL SELECTION

BY
R. A. FISHER, Sc.D., F.R.S.

OXFORD
AT THE CLARENDON PRESS
1930

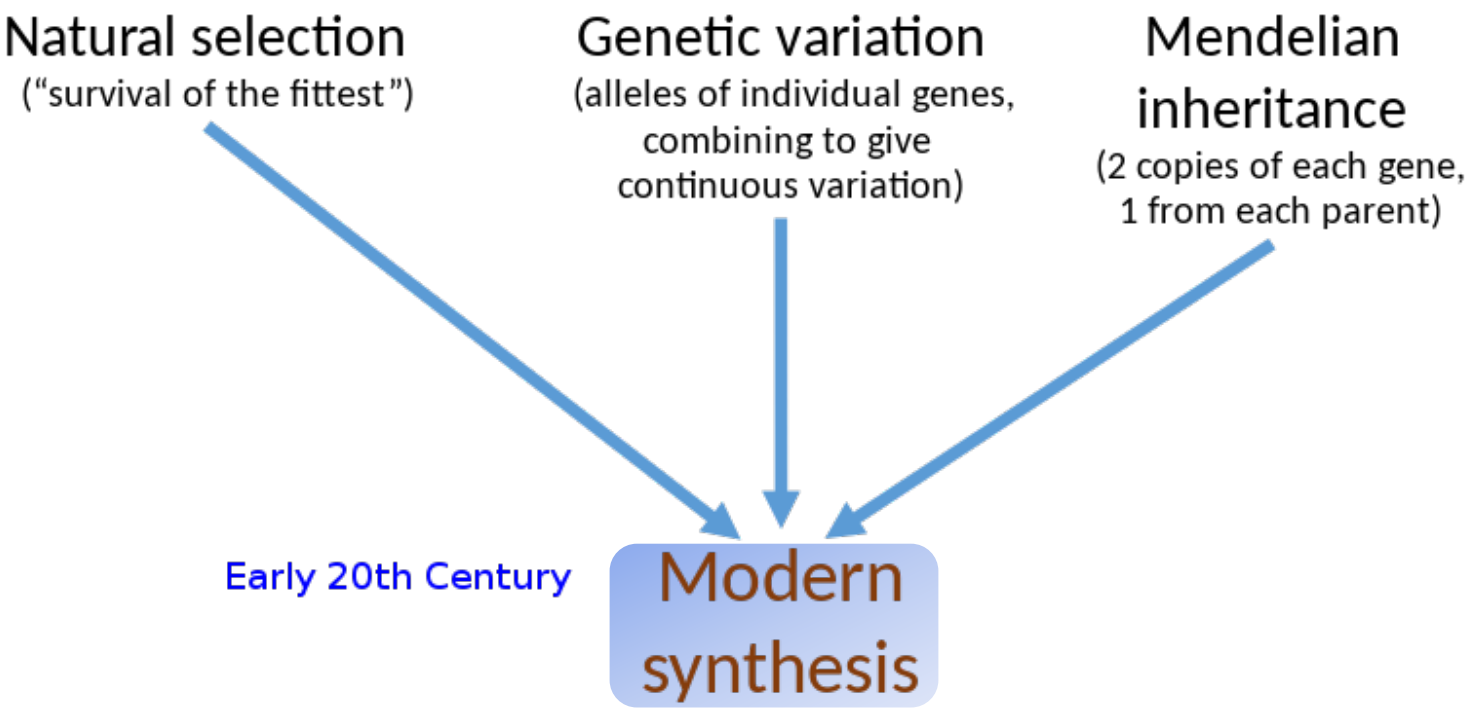






- <u>Continuous variation</u> measured by the biometricians could be produced by the combined action of many discrete genes
- <u>Natural selection</u> could change <u>gene frequencies</u> in a population, resulting in evolution.

- **Background**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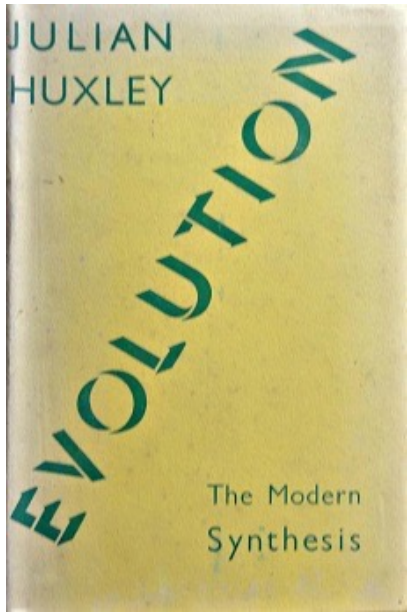
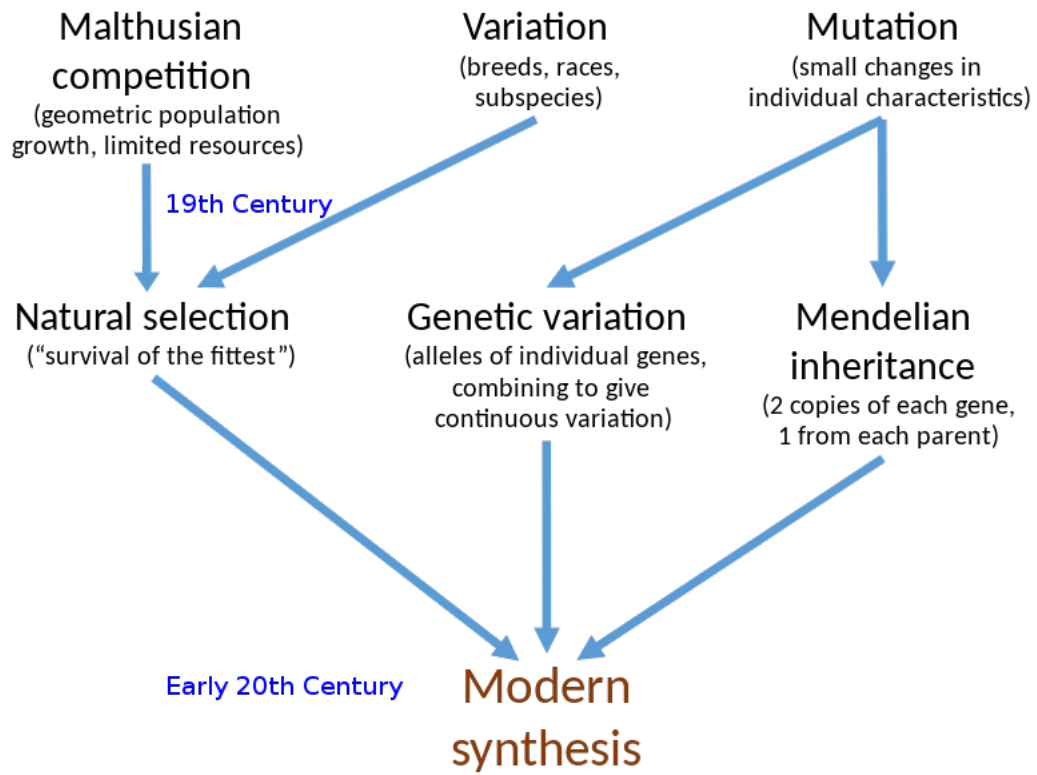
Julian Huxley
(1887-1975)

Son of Thomas Henry Huxley

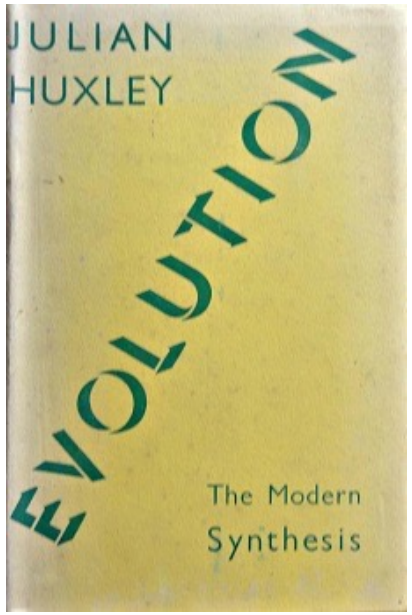


Evolution:
The Modern synthesis
published in 1942



- Several major ideas about evolution came together in the population genetics of the early 20th century to form the modern synthesis of Huxley's title, including **genetic variation**, **natural selection**, and **particulate (Mendelian) inheritance**.
- This ended the eclipse of Darwinism and supplanted a variety of non-Darwinian theories of evolution.

Julian Huxley
(1887-1975)
Son of Thomas Henry Huxley



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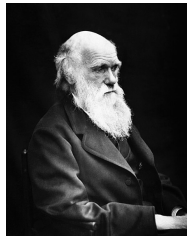
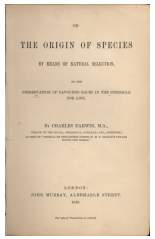
主要观点：

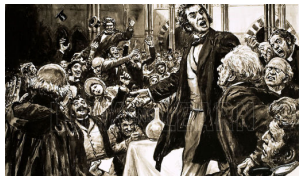
- 种群是生物演化的基本单位
- 生物演化的实质在于种群基因频率的改变。
- 突变和基因重组、自然选择及隔离是物种形成过程的三个基本环节
  - 突变和基因重组产生生物演化的原材料
  - 自然选择使种群的基因频率定向改变并决定生物演化的方向
  - 隔离是新物种形成的必要条件

- **Timeline**

物种起源
自然选择

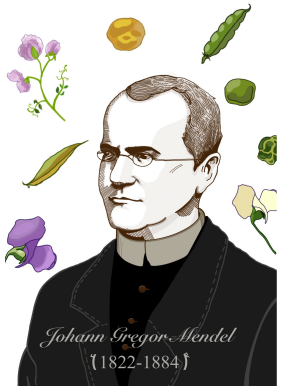
1859



Oxford Evolution Debate

1860

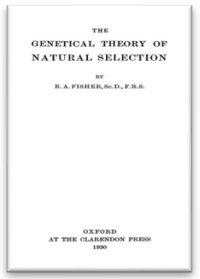
1866



- 分离率
- 自由组合率

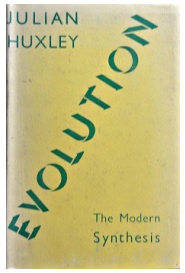
1910

果蝇实验
- 遗传因子（基因）位于染色体上

- *The Genetical Theory of Natural Selection* published

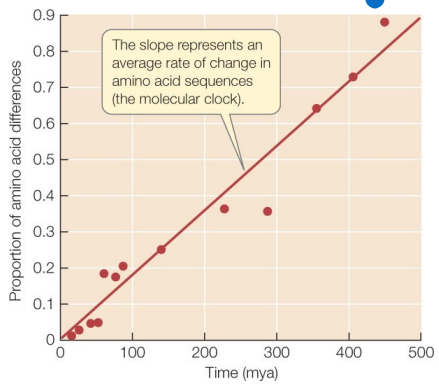
1930

- *Evolution: The Modern synthesis* published

1942

1962

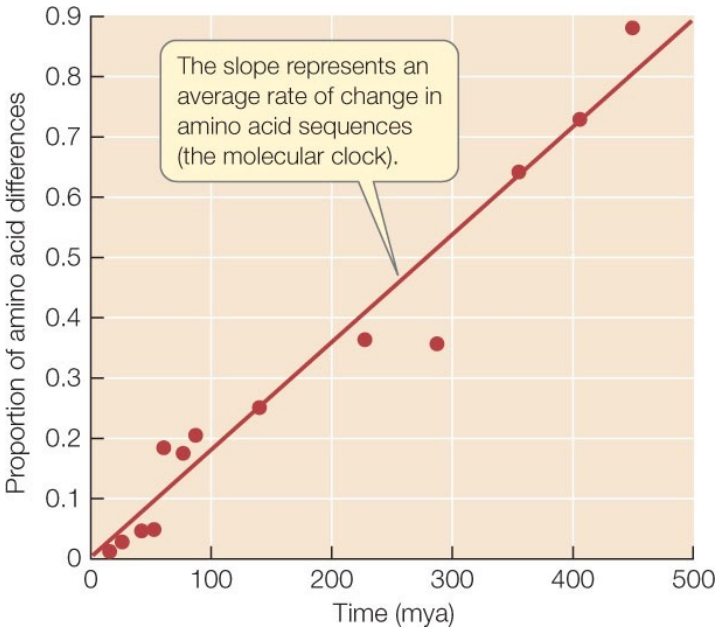


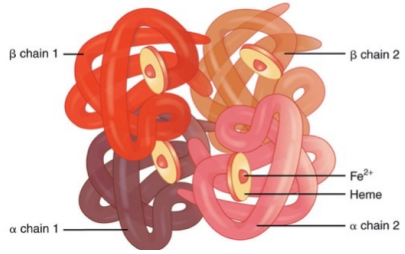
- ***molecular clock***
- ***hemoglobin***

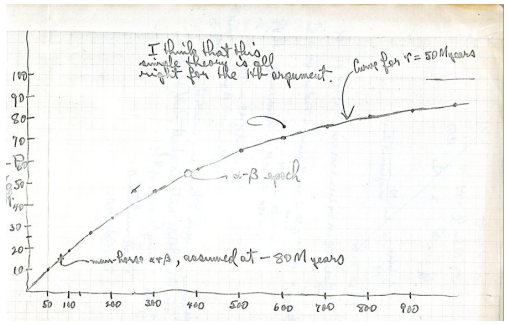

- ***Neutral theory of molecular evolution***
- ***Nearly neutral theory of evolution***

1968 & 1973

1859 1860 1866 1910 1930 1942 1962





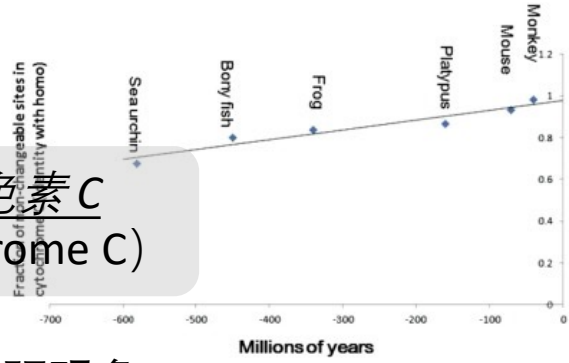


Letter from Linus Pauling to Emile Zuckerkandl

TABLE 1

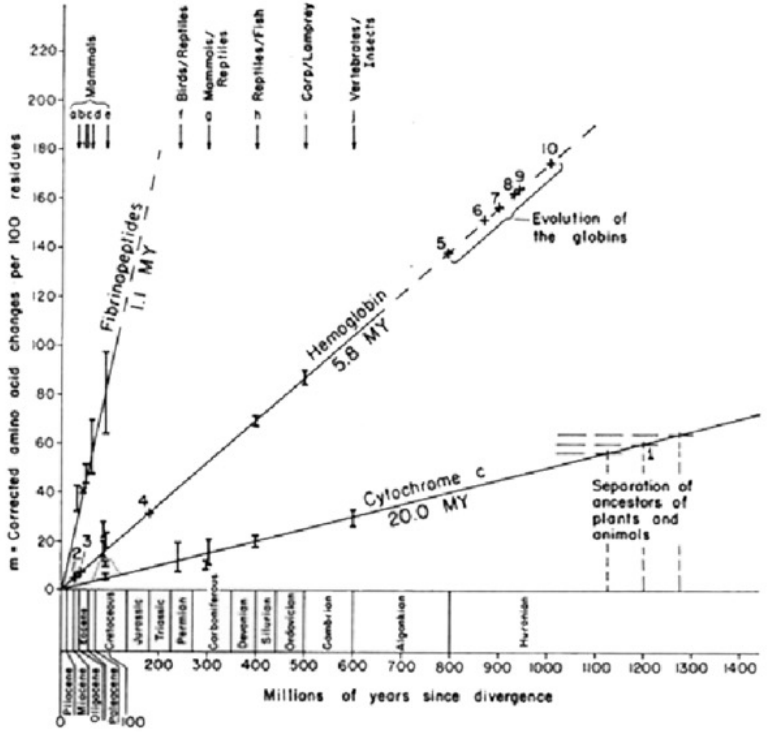
EVOLUTION OF CYTOCHROME *c*

Species comparison	Number of variant residues	Divergence of lines in millions of years
Horse — Man	12	130
Horse — Pig	3	33
Horse — Chicken	12	
Pig — Chicken	10	108–150
Rabbit — Chicken	11	
Man — Chicken	14	
Horse — Tuna	19	
Pig — Tuna	17	
Rabbit — Tuna	19	
Man — Tuna	21	
Chicken — Tuna	18	
Horse — Yeast	44	
Pig — Yeast	43	
Rabbit — Yeast	45	
Man — Yeast	43	
Chicken — Yeast	43	
Tuna — Yeast	48	465–520



细胞色素 C
(Cytochrome C)

- 遗传等距现象



R. E. Dickerson's linear representation of the molecular clock (Dickerson 1971, 37).

- **<u>分子钟</u>**的概念由 Émile Zuckerkandl 和 Linus Pauling 与 *1962* 年首次提出
- 结合化石证据，不同谱系之间*<u>血红蛋白</u>*(Hemoglobin)中氨基酸差异的数量占比随着物种分歧时间大致呈线性关系。

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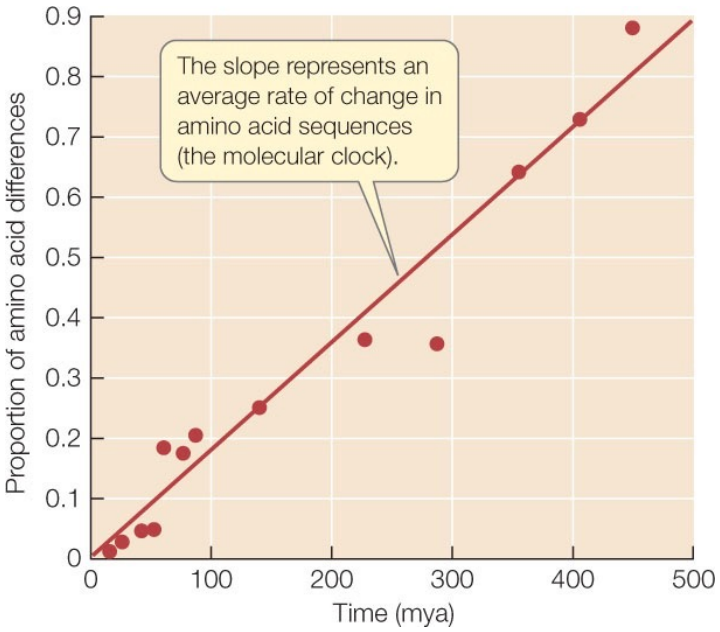

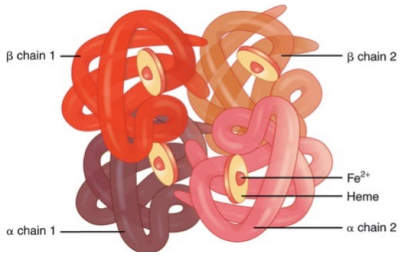

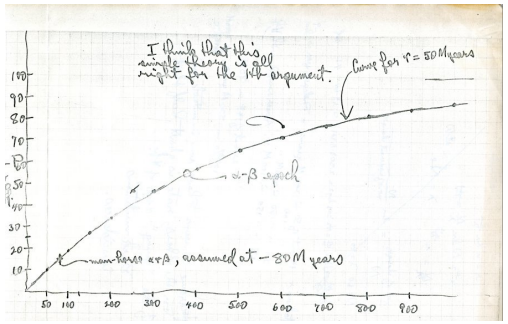

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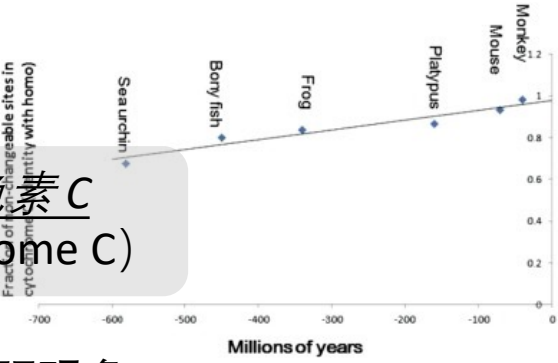

细胞色素 C
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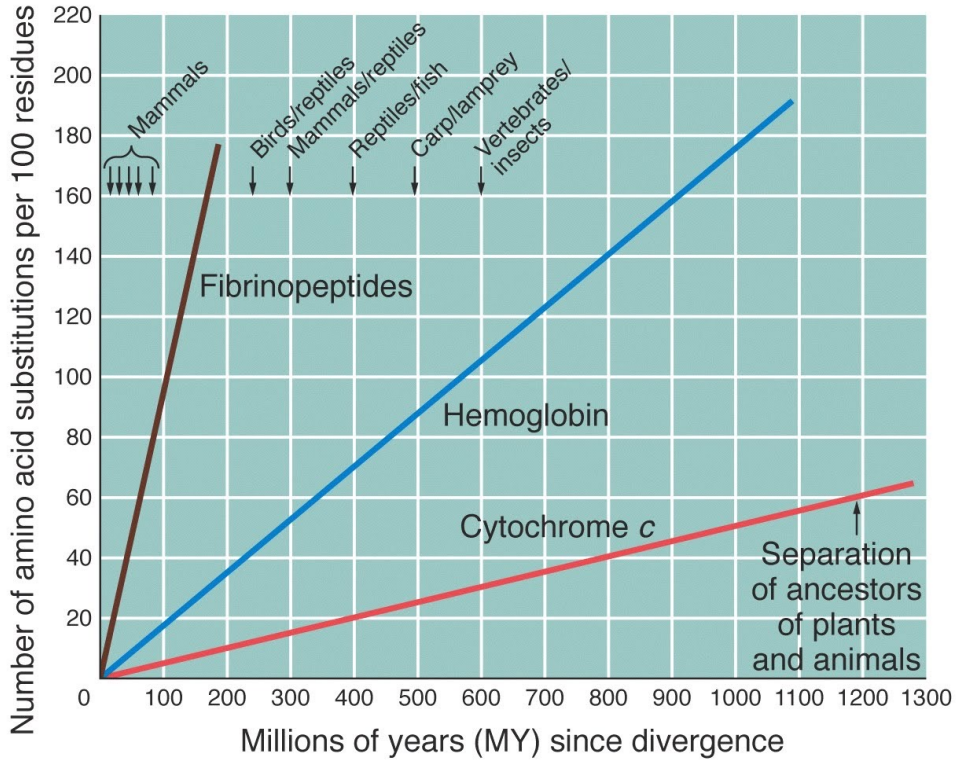

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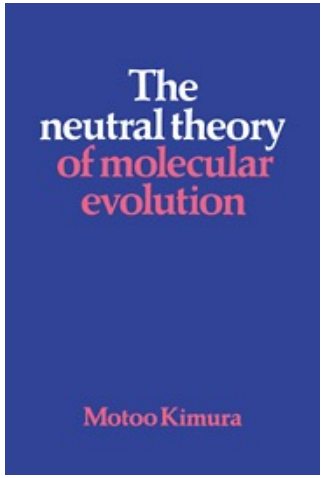
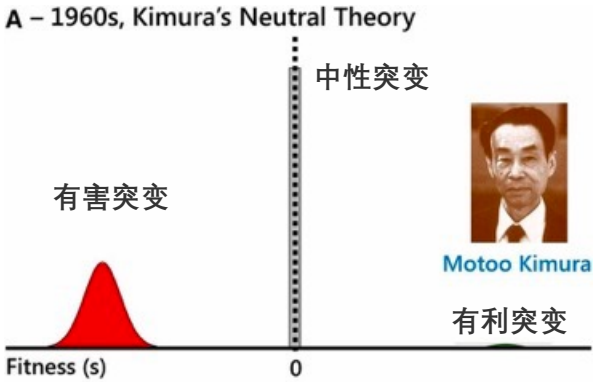
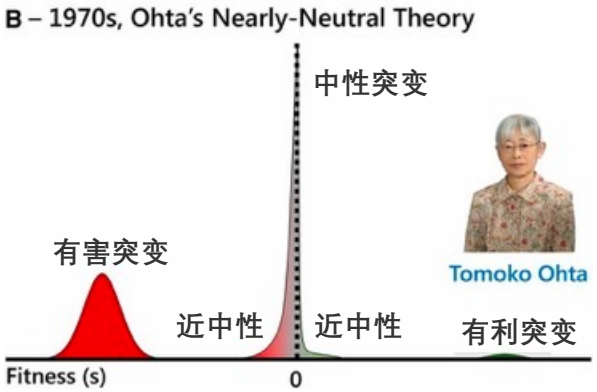
- **1968**

木村资生
Motoo Kimura



中性理论





- **1973**

太田朋子
Tomoko Ohta

近中性理论

nature › letters › article

Published: 09 November 1973

Slightly Deleterious Mutant Substitutions in Evolution

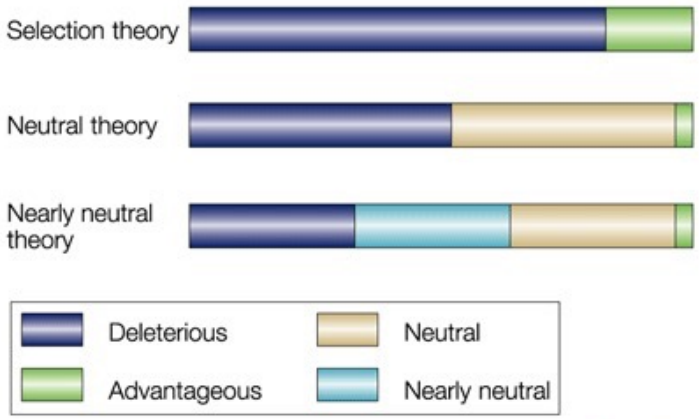
TOMOKO OHTA

Nature **246**, 96–98 (1973) | Cite this article

3575 Accesses | **639** Citations | **33** Altmetric | Metrics

Abstract

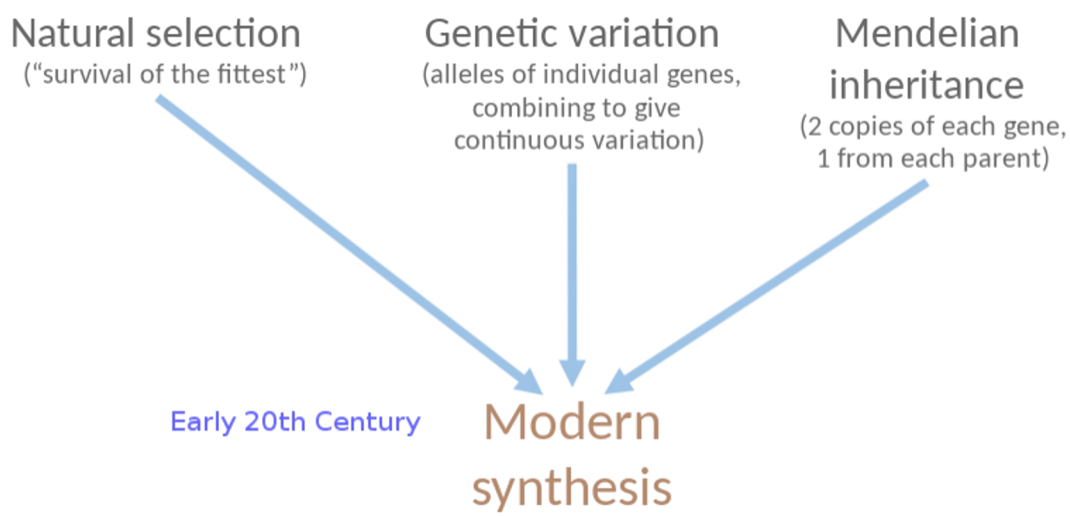
RECENT advances in molecular genetics have had a great deal of influence on evolutionary theory, and in particular, the neutral mutation-random drift hypothesis of molecular evolution[1,2] has stimulated much interest. The concept of neutral mutant substitution in the population by random genetic drift can be extended to include random fixation of very slightly deleterious mutations which have more chance of being selected against than of being selected for[3,4]. If this class of mutant substitution is important, we can predict that the evolution is rapid in small populations or at the time of speciation[5]. Here I shall organize the observed facts which indicate that this class is in fact important.



- **Background**

Standard evolutionary theory, SET

*"Standard evolutionary theory is **gene-centered**, and treats as evolutionary processes solely those events that change gene frequencies"*



主要因素：

1.Mutation: *introduces new variants at random. Repeated occurrence of the same genetic variants is called mutation pressure.*

2.Natural selection: *makes adaptive variants more common through differential survival and reproduction.*

3.Genetic drift: *random changes in frequency of genetic variants due to sampling.*

4.Gene flow: *variants enter and leave a population via migration, dispersal or mating.*

- **1952**

突变的随机性

The Lederberg experiment

1. Bacteria are spread out on a plate, called the “original plate.”

2. They are allowed to grow into several different colonies.

3. This layout of colonies is stamped from the original plate onto a new plate that contains the antibiotic penicillin.

4. Colonies X and Y on the stamped plate survive. They must carry a mutation for penicillin resistance.

The answer is **no**:
When the original plate is washed with penicillin, the same colonies (those in position X and Y) live — even though these colonies on the original plate have never encountered penicillin before.

The Lederbergs set out to answer the question:
“Did the colonies on the new plate evolve antibiotic resistance because they were exposed to penicillin?”

- **1993**

突变的随机性

ARTICLES

The Directed Mutation Controversy and Neo-Darwinism

Richard E. Lenski and John E. Mittler

According to neo-Darwinian theory, random mutation produces genetic differences among organisms whereas natural selection tends to increase the frequency of advantageous alleles. However, several recent papers claim that certain mutations in bacteria and yeast occur at much higher rates specifically when the mutant phenotypes are advantageous. Various molecular models have been proposed that might explain these directed mutations, but the models have not been confirmed. Critics contend that studies purporting to demonstrate directed mutation lack certain controls and fail to account adequately for population dynamics. Further experiments that address these criticisms do not support the existence of directed mutations.

A fundamental tenet of evolutionary biology is that mutations are random events. This tenet does not mean that mutation rates are unaffected by environmental factors or that all portions of the genome are equally susceptible to mutation. Indeed, enzymes that catalyze certain DNA repair processes are regulated by environmental factors, and many mutations are mediated by mobile elements that are not uniformly distributed in the genome (*1, 2*). Rather, the randomness of mutation refers to the supposition that the likelihood of any particular mutational event is independent of its specific value to the organism (*3*).

suggesting that cells may have mechanisms for choosing which mutations will occur," which provoked vigorous discussion among biologists and philosophers of science (*8–13*). Subsequent studies (*14–22*) have also suggested that certain mutations occur more often when the resulting phenotype is advantageous, and such mutations have been variously described as directed, Cairnsian, adaptive, or selection-induced.

In this paper, we review the history and current status of the controversy, including key experimental findings, alternative explanations for these findings, and their relationship to neo-Darwinism. The hypoth-

But bacteriologists could neither see individual mutants nor demonstrate their existence except by imposing selection for the mutant phenotype. Consequently, it was unclear whether selection had caused the mass conversion of cells from one state to another or whether selection had increased the proportion of mutant cells in a population by differential survival and growth.

Strong support that neo-Darwinism could be extended to bacteria came in 1943, when Luria and Delbrück devised the fluctuation test (*26*). They formulated two alternative hypotheses to account for the appearance of bacteria resistant to infection by viruses. Under the hypothesis of random mutation, each bacterium has some probability of spontaneously mutating from a viral sensitive to a viral resistant state, even in the absence of virus. Under the hypothesis of directed mutation (which Luria and Delbrück called "acquired hereditary immunity"), each bacterium has some chance of surviving and becoming resistant to viral attack. Under both hypotheses, resistance is inherited. The critical distinction between these models is that, in bacterial

- 基因突变是随机事件，这是演化论基本原理之一。
- 随机并不是指突变频率不受环境影响，也不是在说基因组的所有位置发生突变的概率都相同。
- 突变的随机性指的是某个突变对于生物的价值不会影响其出现的概率。

Lenski RE, Mittler JE. 1993. The directed mutation controversy and neo-Darwinism. Science 259: 188–94.

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- 饶毅. 孤独的天才

浙江大学
生命演化研究中心

谢谢！

The introduction of
Standard Evolutionary Theory (SET)
--Modern Synthesis

卢妍林 & 陈光霁
2022年9月17日