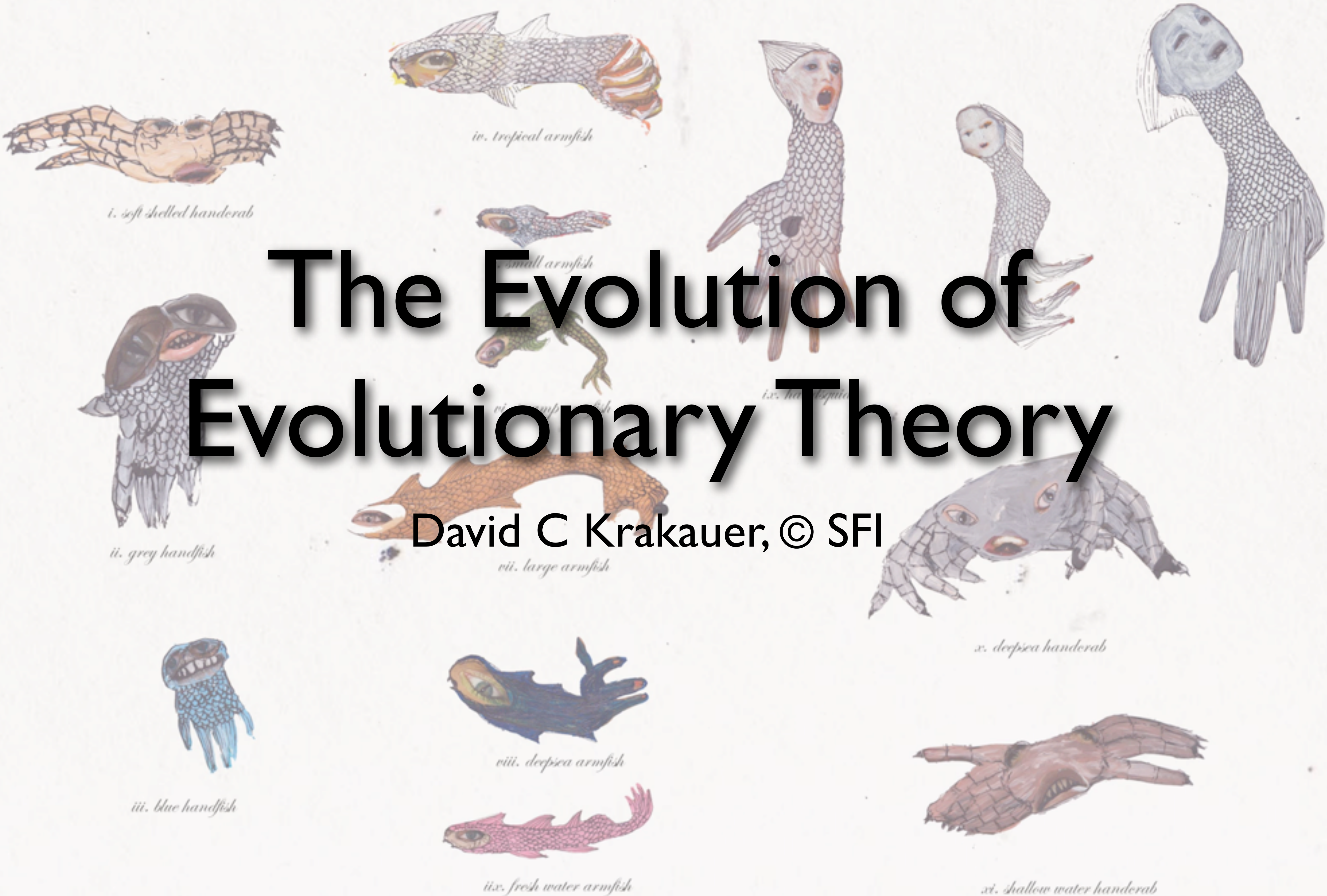
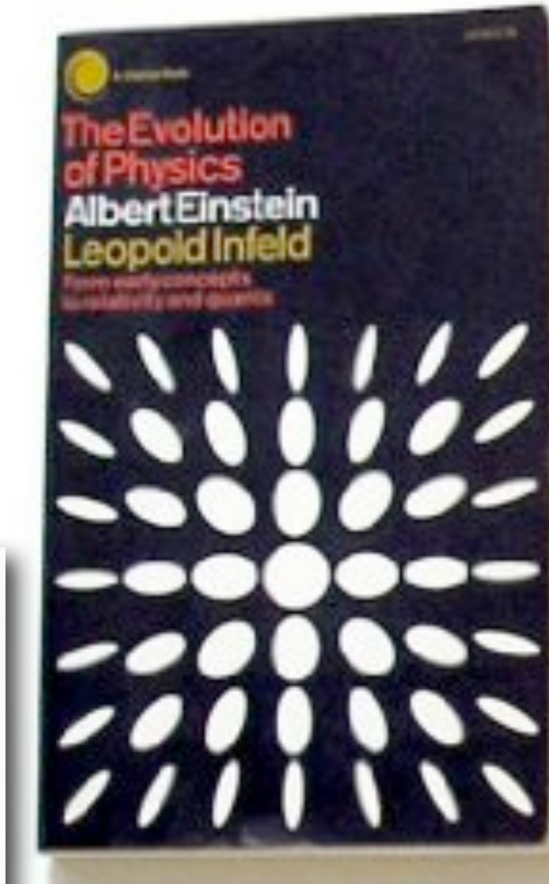


The Evolution of Evolutionary Theory

David C Krakauer, © SFI

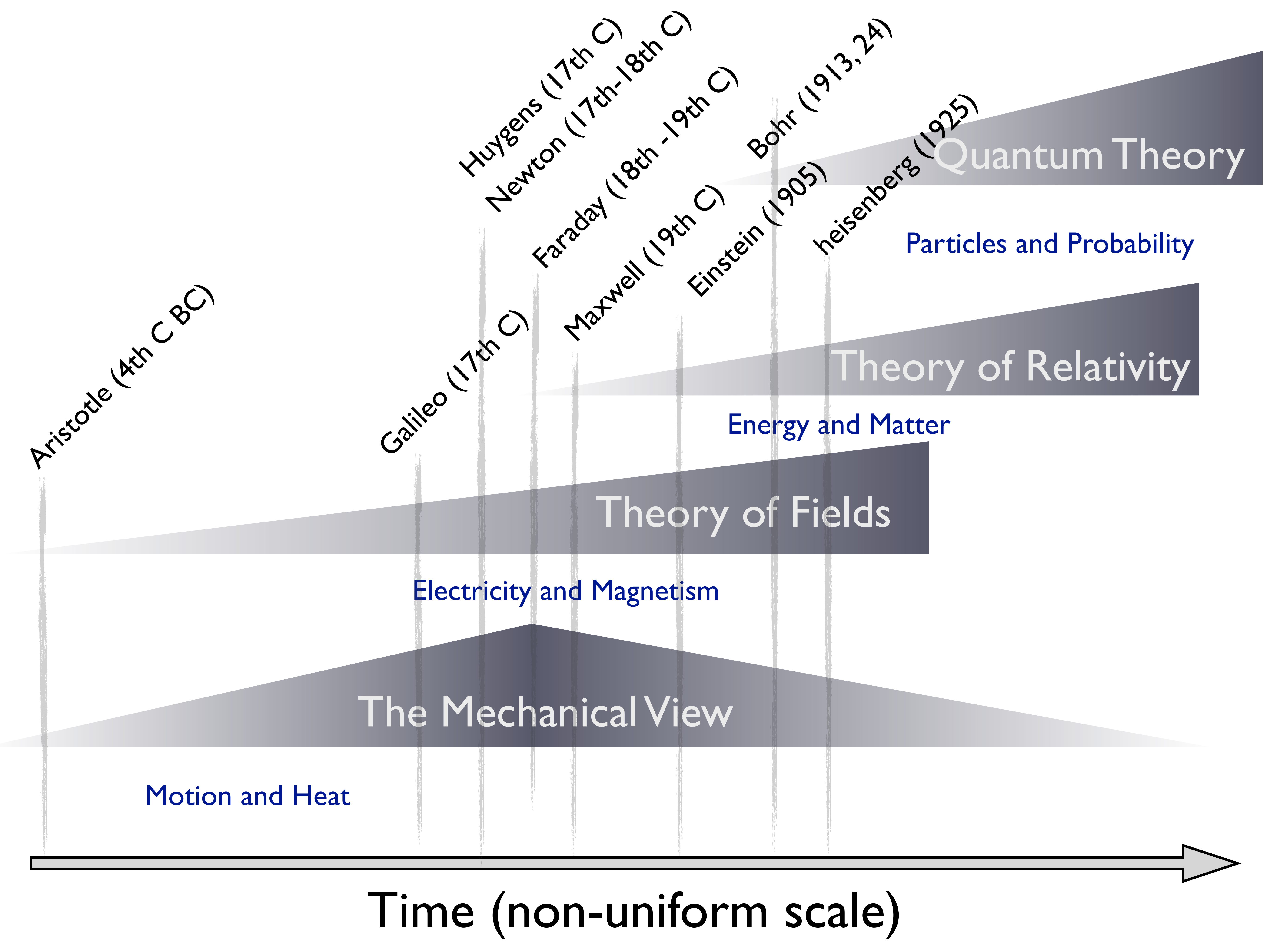


1938

- "Techniques of investigation, systematic methods for finding and following clues"
- "False clues murder the story..."
- Clues are often "strange, incoherent, and wholly unrelated"
- "The method of reasoning directed by intuition was wrong and lead to false ideas"
- "Galileo's contribution was to destroy intuition, and replace it by a new [formal] one"

“"I believe that pipe smoking contributes to a somewhat calm and objective judgment in all human affairs”
Albert Einstein 1950.

“It is quite a three pipe problem, and I beg that you won't speak to me for fifty minutes.”
Sherlock Holmes 1891


Aristotle (4th C BC)
Galileo (17th C)
Huygens (17th C)
Newton (17th-18th C)
Faraday (18th -19th C)
Maxwell (19th C)
Einstein (1905)
Bohr (1913, 24)
heisenberg (1925)
Quantum Theory
Particles and Probability
Theory of Relativity
Energy and Matter
Theory of Fields
Electricity and Magnetism
The Mechanical View
Motion and Heat
Time (non-uniform scale)

What is Evolutionary Theory?

2000

1990

1930

1859

- A Physics-like theory searching for Laws?
- A Statistical/Inferential Theory like Bayesian learning or approximate dynamic programming?
- An algorithmic/computational optimization theory?
- A dynamical process constrained by inheritance, mutation and selection?
- A narrative, historical description of life on earth structured by a plot called natural selection.

micro-Evolution of Theory

Inheritance

Selection

Levels

Development

- Blending Inheritance & Genetic Inheritance — Biometricians versus mendelians
- Balancing Selection & the Neutral Theory — Selectionists versus neutralists
- Group Selection & Kin Selection — Levels of selection debate
- Phyletic Gradualism & Punctuated Equilibrium — Micro versus Macroevolutionists

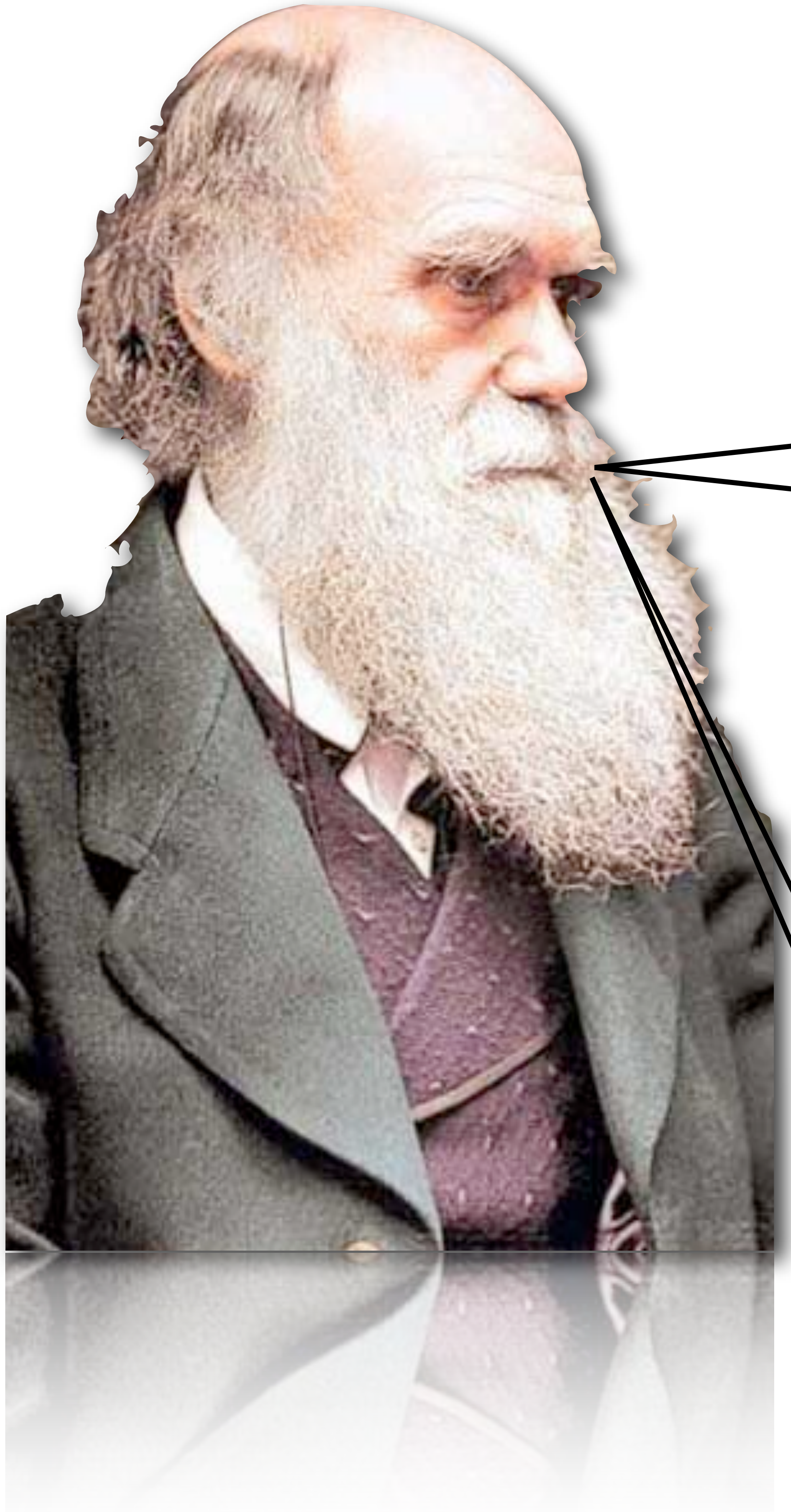
Nature of Inheritance

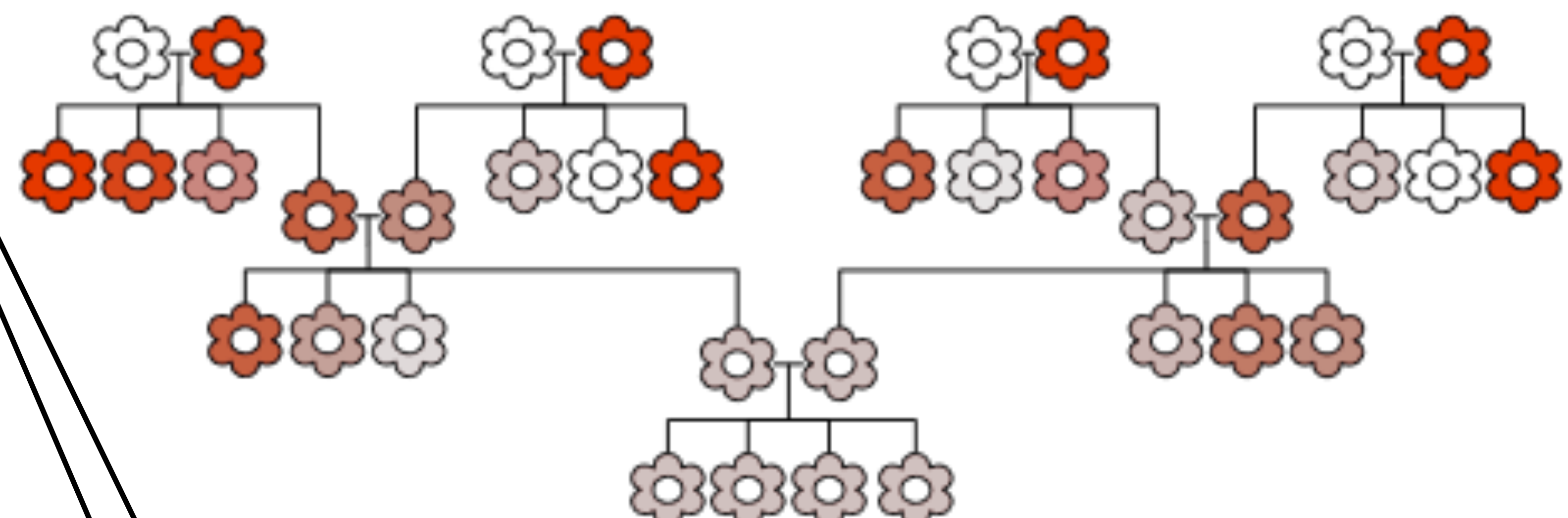
<u>Intuition</u> - Continuous inheritance

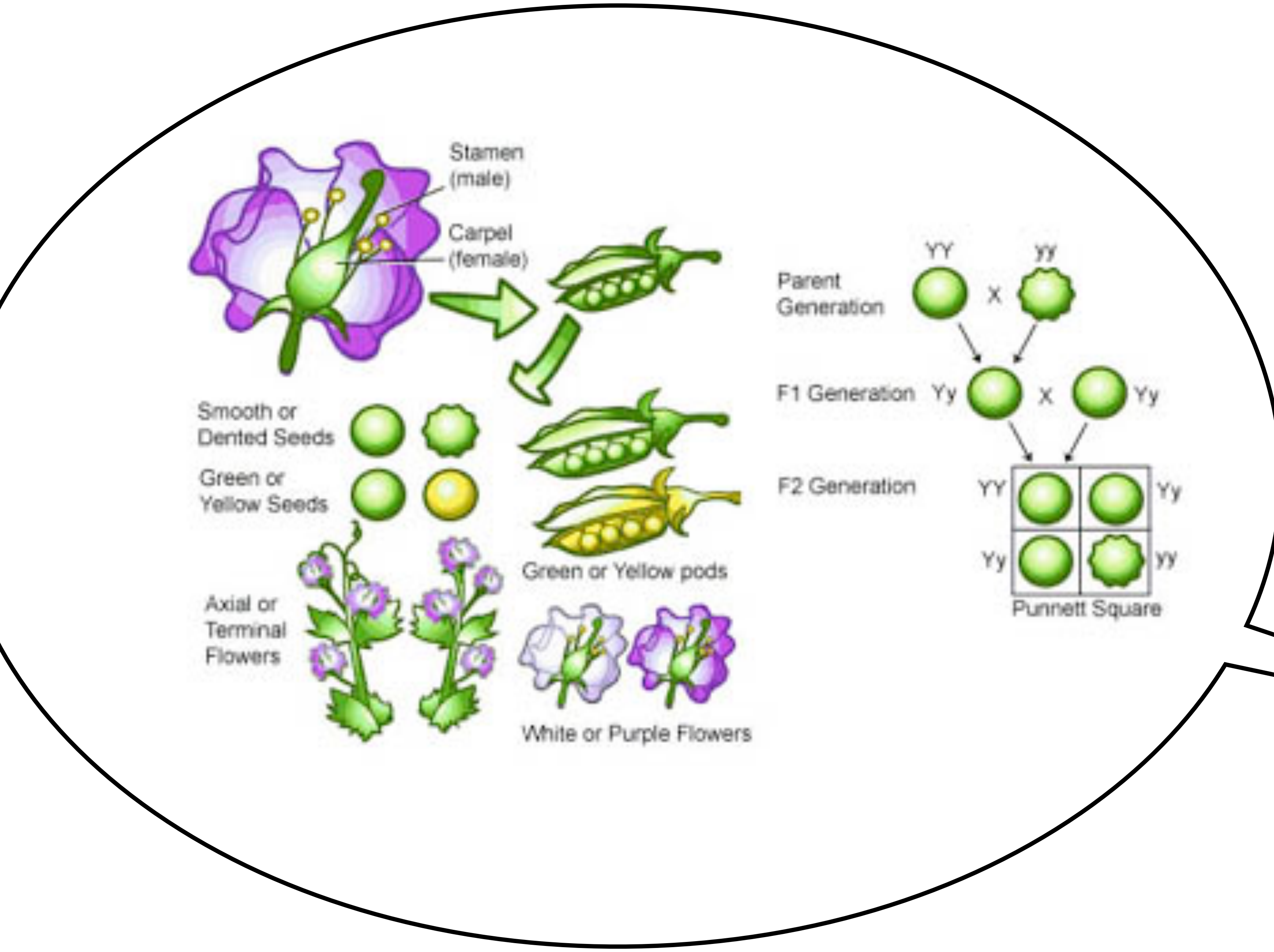
<u>False Clue</u> - Quantitative traits

<u>Anomalous Observation</u> - Discrete traits

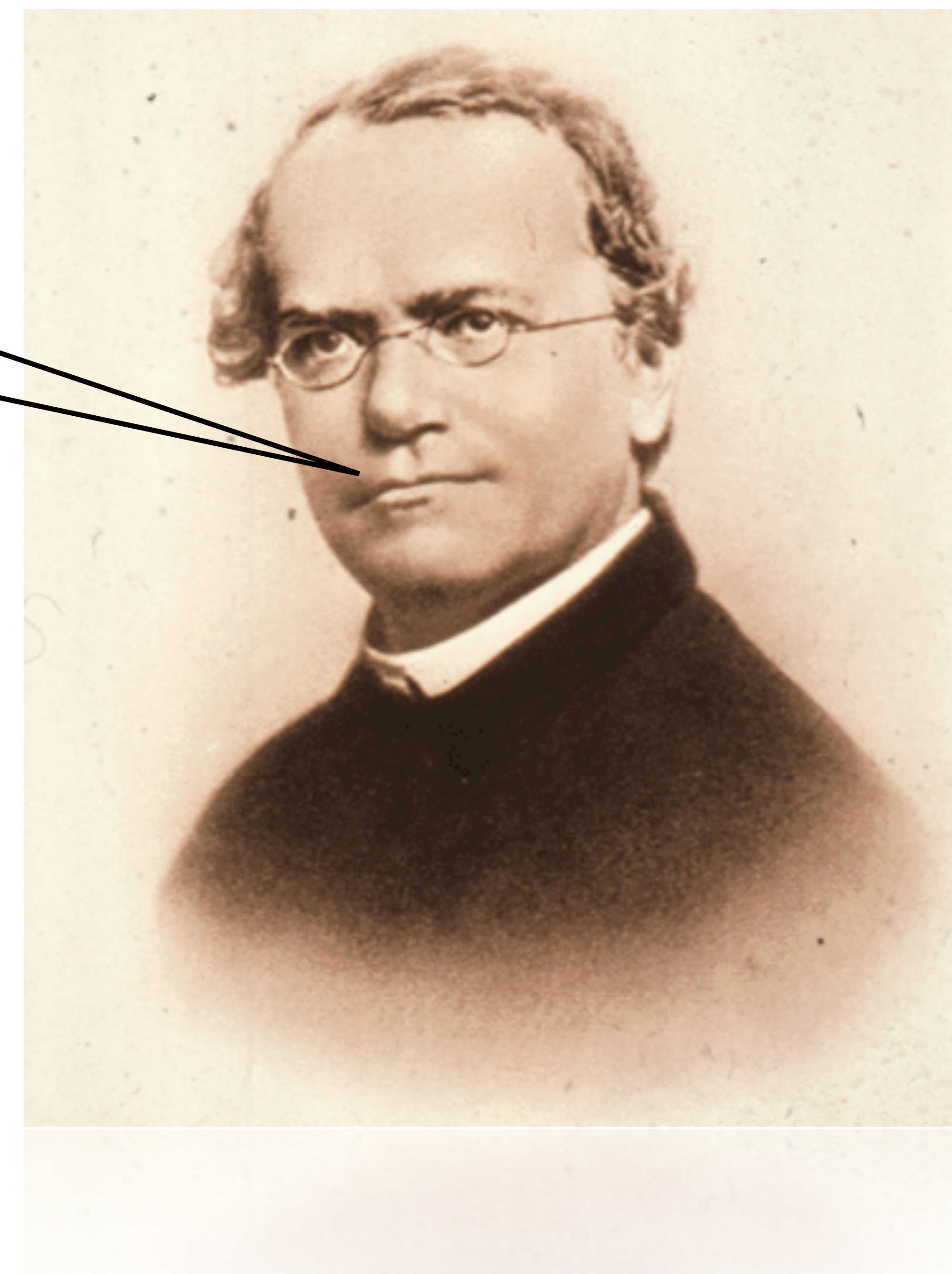
<u>Techniques of Investigation</u> - Statistics/Biometry


"Crossing plays a very important part in nature keeping individuals in the same species..true and uniform to character" (1842)
"Natura non facit saltum"

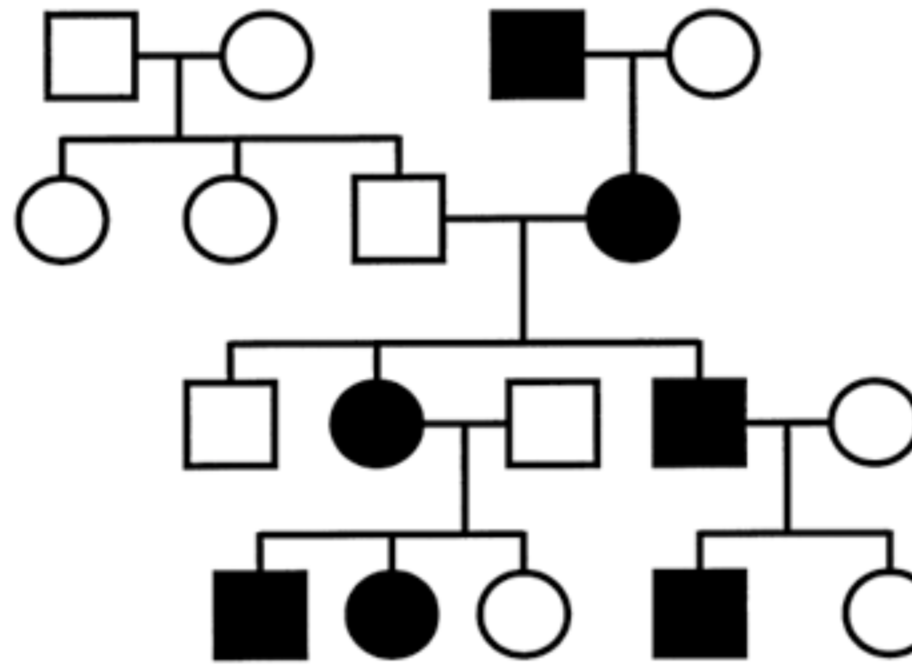




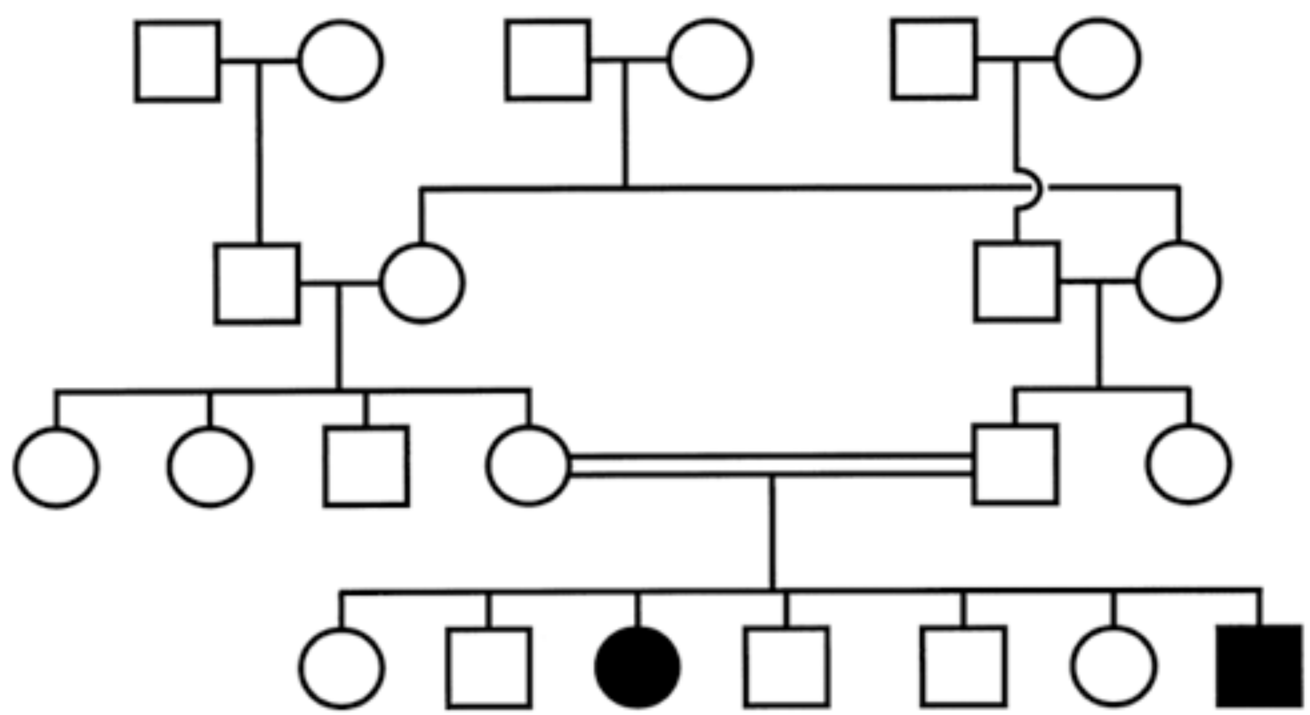
Stamen
(male)
Carpel
(female)
Smooth or
Dented Seeds
Green or
Yellow Seeds
Axial or
Terminal
Flowers
Green or Yellow pods
White or Purple Flowers
Parent
Generation
YY
yy
X
F1 Generation
Yy
X
Yy
F2 Generation
YY
Yy
Yy
yy
Punnett Square



Autosomal dominant

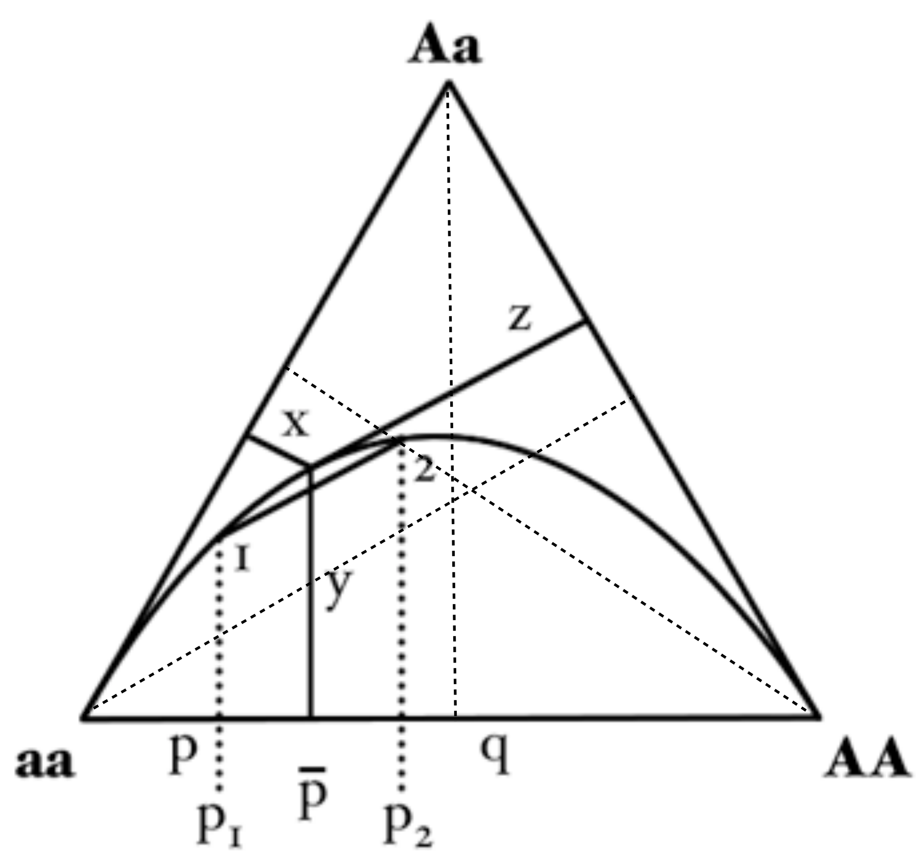


Autosomal recessive

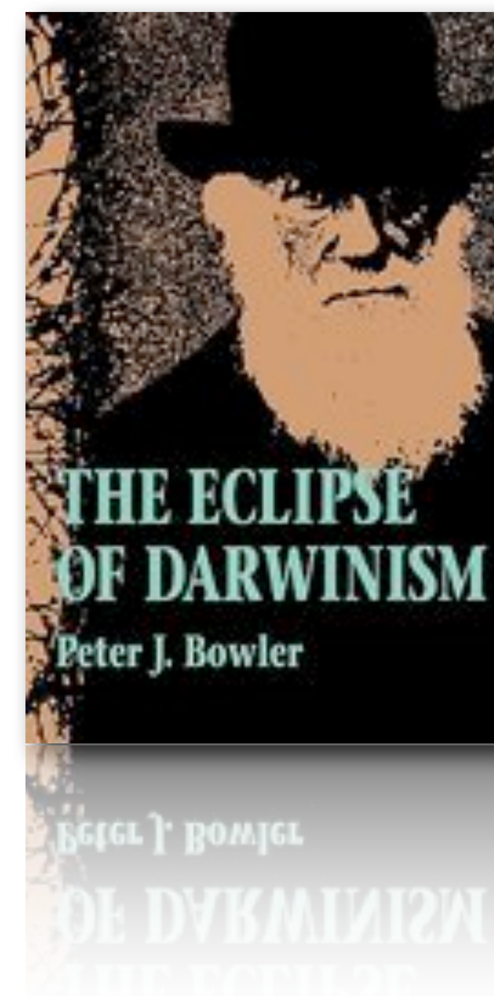


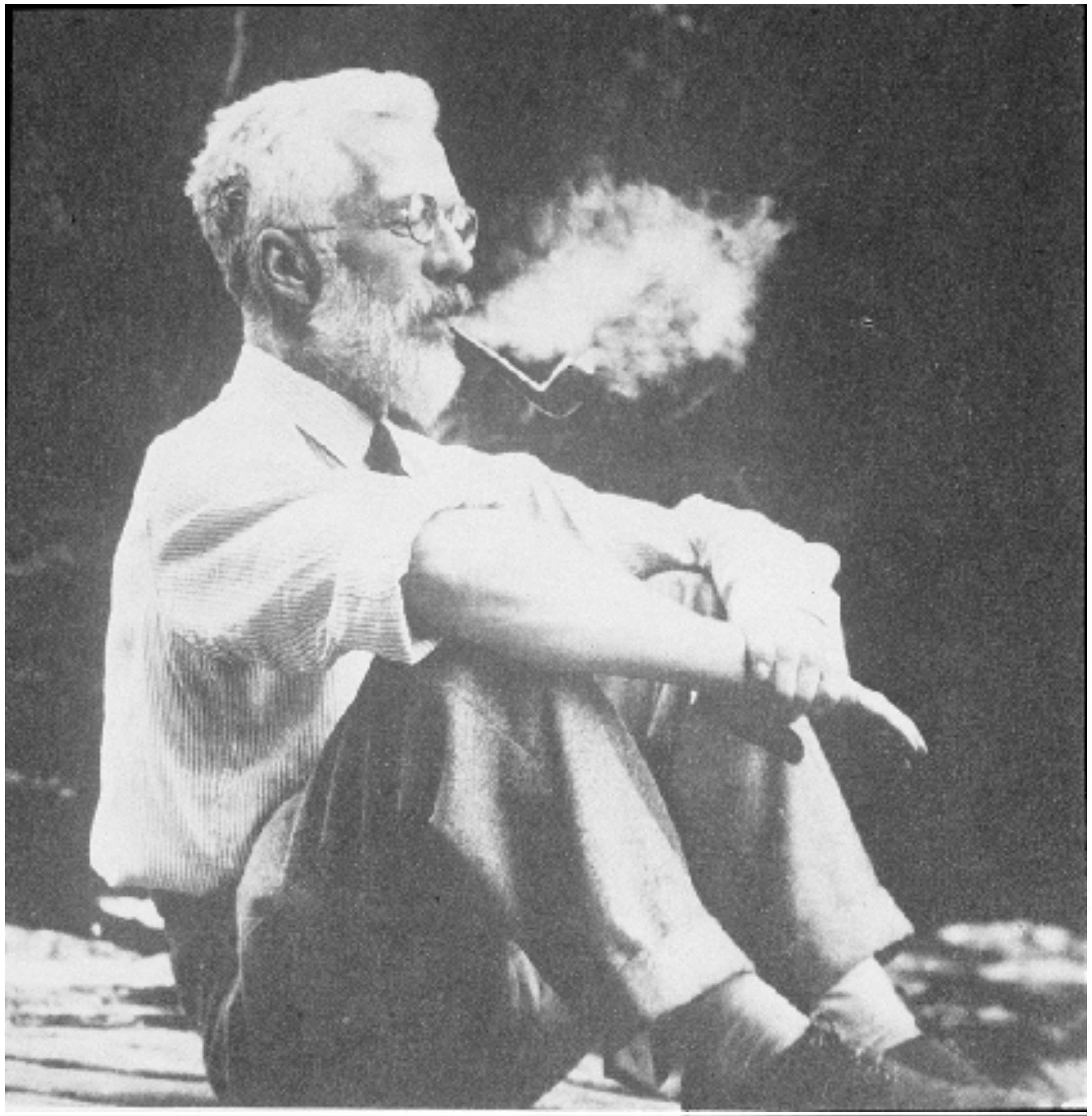
Hardy-Weinberg Equilibrium

$$p(A) = p; p(a) = q$$
$$p^2 + 2pq + q^2 = 1$$



de Finnetti diagram with
1 bi-allellic loci



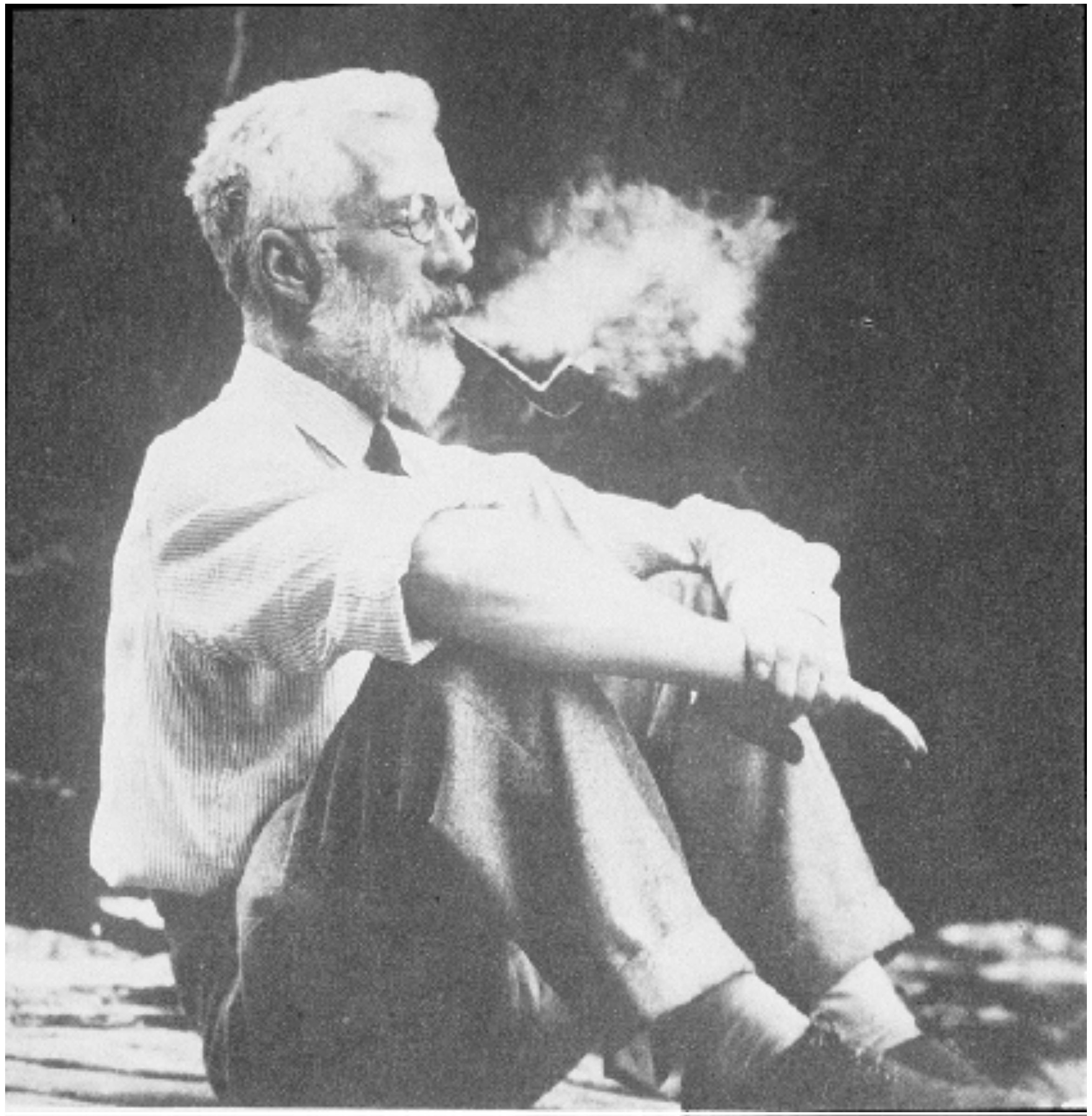


Ronald Alymer Fisher

- *The correlation among relatives on the supposition of Mendelian Inheritance* (1918)
- Rejected From Proceedings Royal Society
- Published in Royal Society of Edinburgh

“several attempts have been made to interpret the well-established results of biometry with the Mendelian scheme of inheritance”

“For stature the coefficient of correlation between brothers is .54... It is not sufficient to ascribe this last residue (46%) to the effects of the environment”



Ronald Alymer Fisher

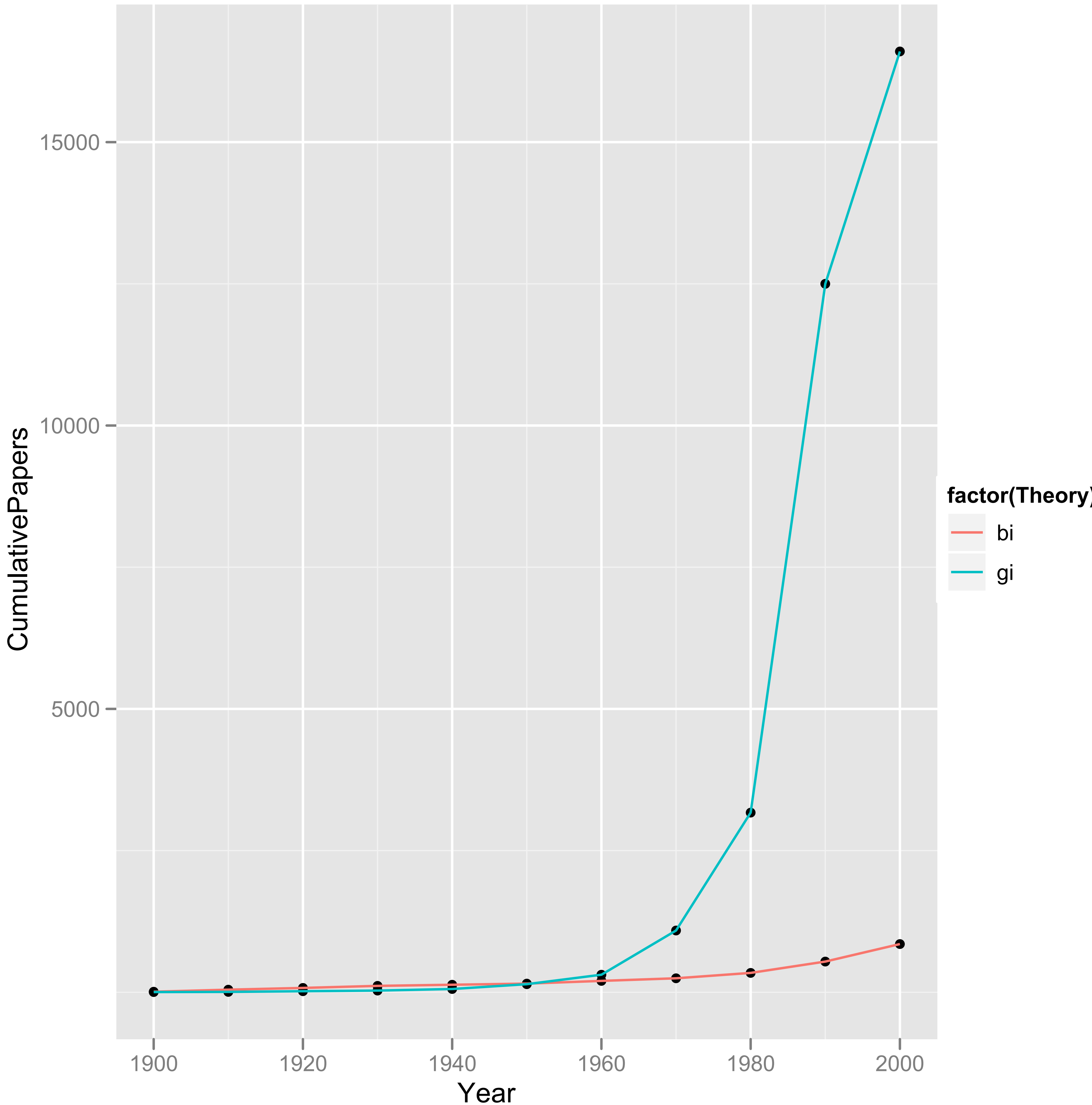
- Introduced the concept of Variance etc.

$$\sigma_z = \sigma_x^2 + \sigma_y^2$$

- “The simplest hypothesis is that...features are determined by many Mendelian factors” from heterozygous parents, and many of these factors interact “non-additively”

$$\sigma_z = \sum_i^N \sigma_i^2 + f(\overrightarrow{\sigma}_{j \setminus N})$$

- Dominance is often incomplete in heterozygotes - leaving around 5% for the environment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Paradoxes of Selection and Dominance

<u>Intuition</u> - Selection Preserves Variability
<u>False Clue</u> - Balancing Selection
<u>Anomalous Observation</u> - Rampant polymorphism
<u>Techniques of Investigation</u> - Diffusion theory/Neutral Theory

Heterosis/Overdominance

$$w(Aa) = 1$$

$$w(AA) = 1 - s_A$$

$$w(aa) = 1 - s_a$$

Polymorphism maintained by high mortality

$$\bar{q}_a = \frac{s_A}{s_a + s_A}$$

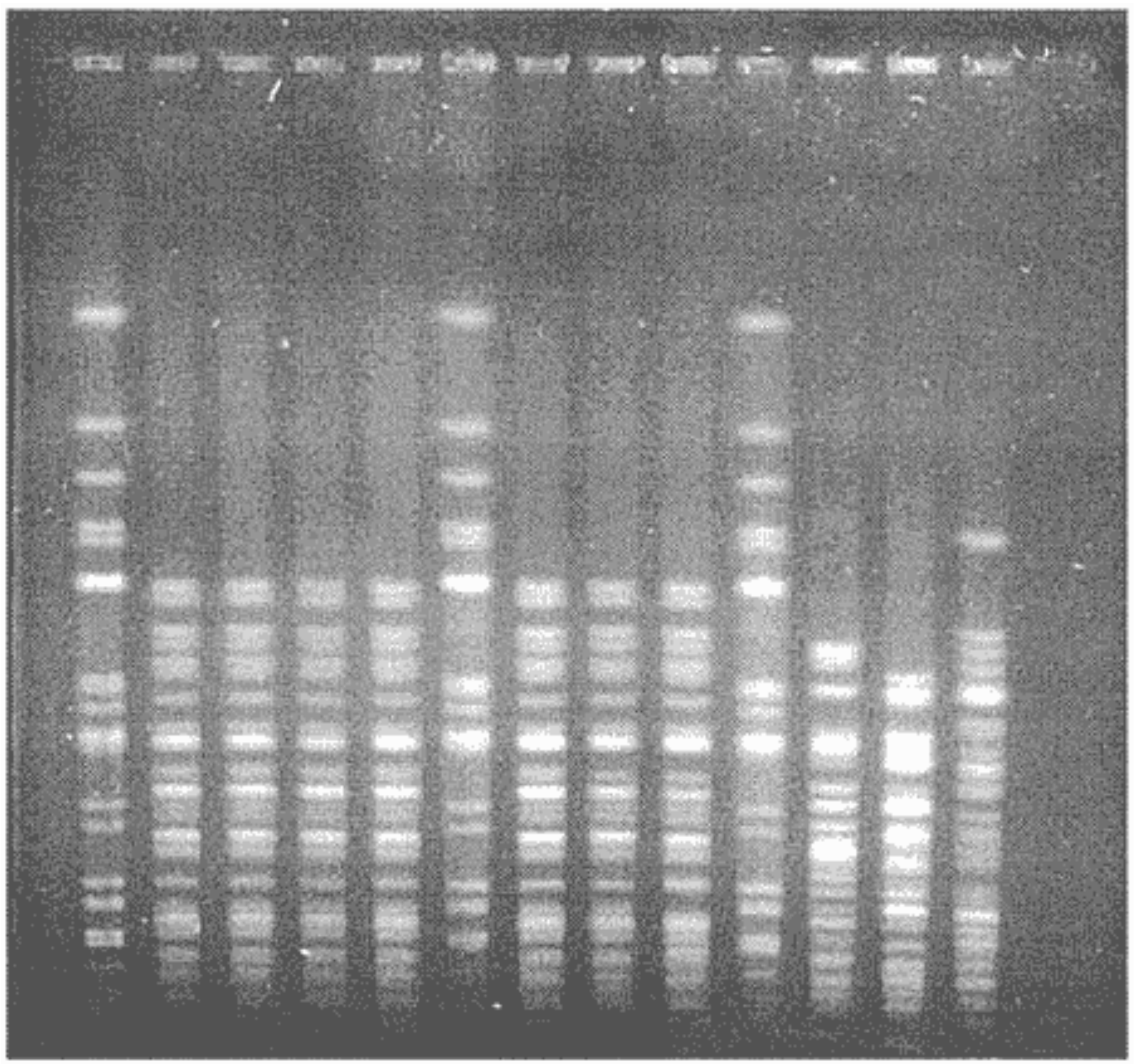
$$\bar{w} = 1 - \frac{s_A s_a}{s_A + s_a}$$

30% sub-saharan Africa

The Paradox of Excessive Electrophoretic Allozyme Polymorphism

Lewonting & Hubby 1966

30% of 18 loci polymorphic



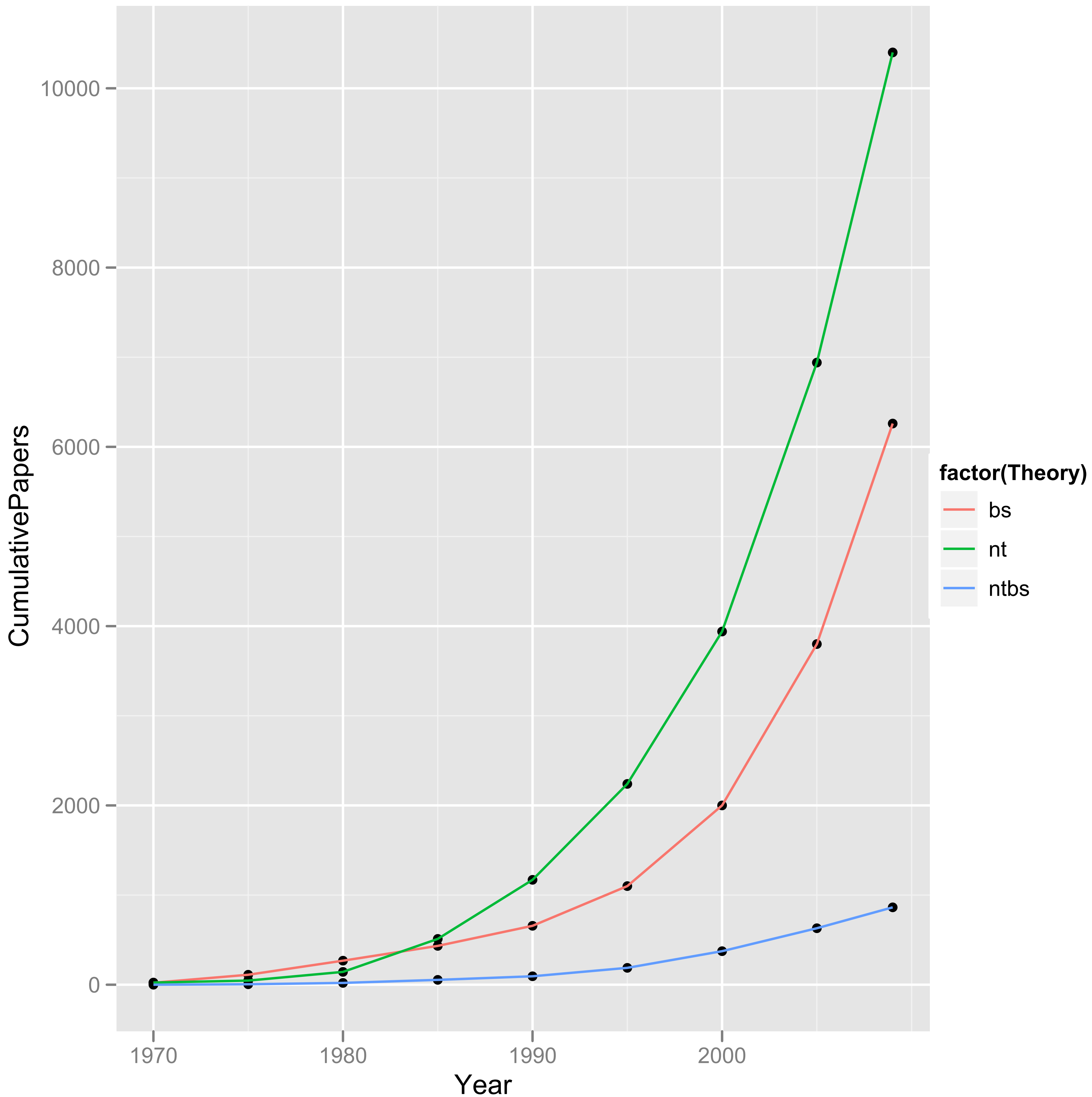
$$\bar{w} = 1 - \frac{s_A s_a}{s_A + s_a}$$

Neutral & Near Neutral Theory

Motoo Kimura

- “Genetic Variability maintained in a finite population due to mutational production of neutral and nearly neutral isoalleles” (1968)
- If the possible number of alleles is large, the effective number observed will be:

$$n_e = 4N_e\mu + 1$$



CumulativePapers
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2000
0
1970
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1990
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Year
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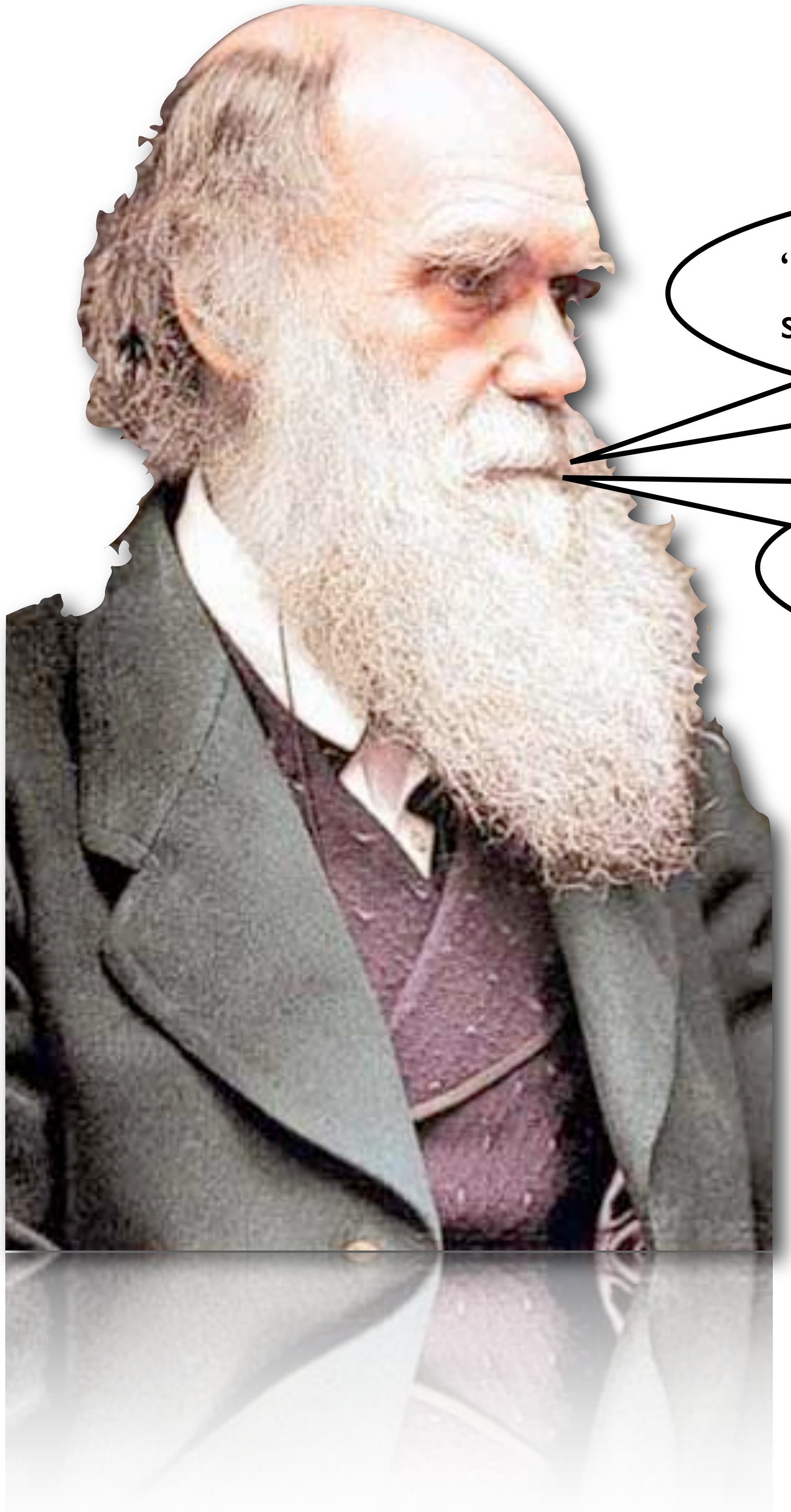
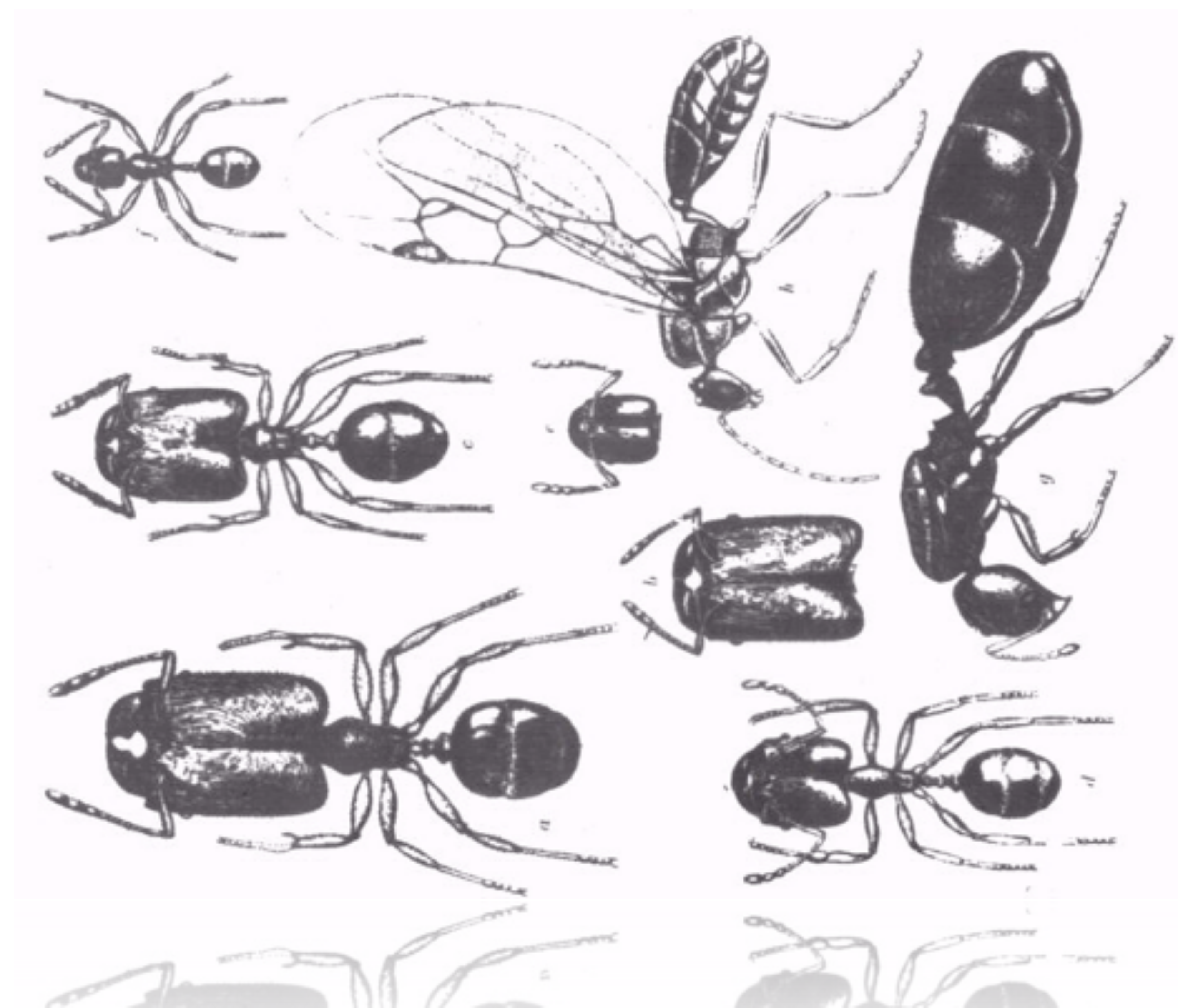
Individuality & Levels of Selection

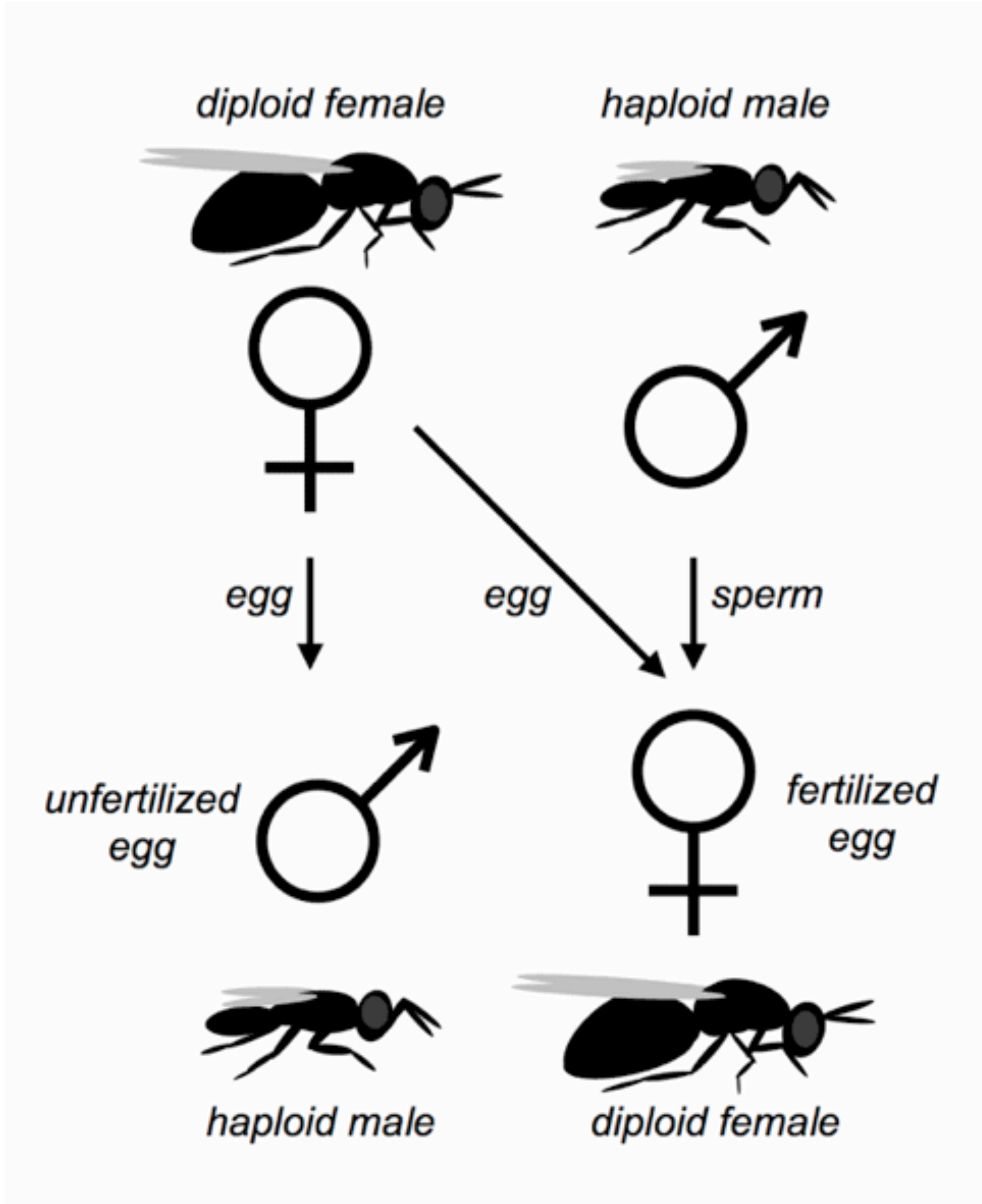
<u>Intuition</u> - Individuals as evolutionary units
<u>False Clue</u> - Mendelian segregation
<u>Anomalous Observation</u> - Altruism
<u>Techniques of Investigation</u> - Stochastic Processes/Kin selection


"Objections to the theory of natural selection and instinct: neuter and sterile insects"
"selection may be applied to the family, as well as the individual and may thus gain the desired end"



Greater generality arrived at through observational anomalies

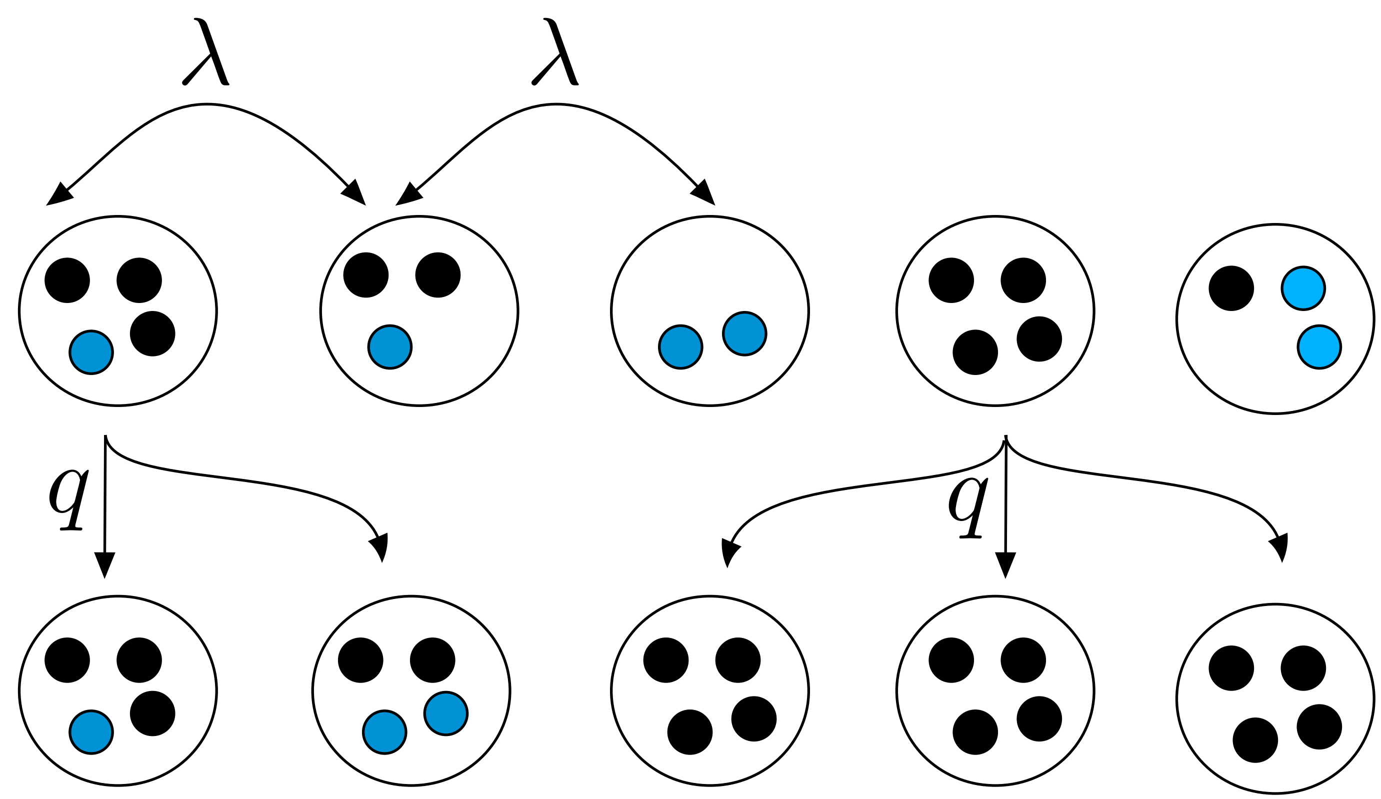
"Clues are often strange, incoherent, and wholly unrelated"


diploid female
haploid male
egg
egg
sperm
unfertilized egg
fertilized egg
haploid male
diploid female

Kin/Group Selection

$n = 4$ $\qquad$ $n_g = 5$

$r_i = f(\pi_i)$



$\pi_i({\color{blue}\bullet}, \bullet) = b/(n-1)$

$\pi_j(\bullet, {\color{blue}\bullet}) = -c$

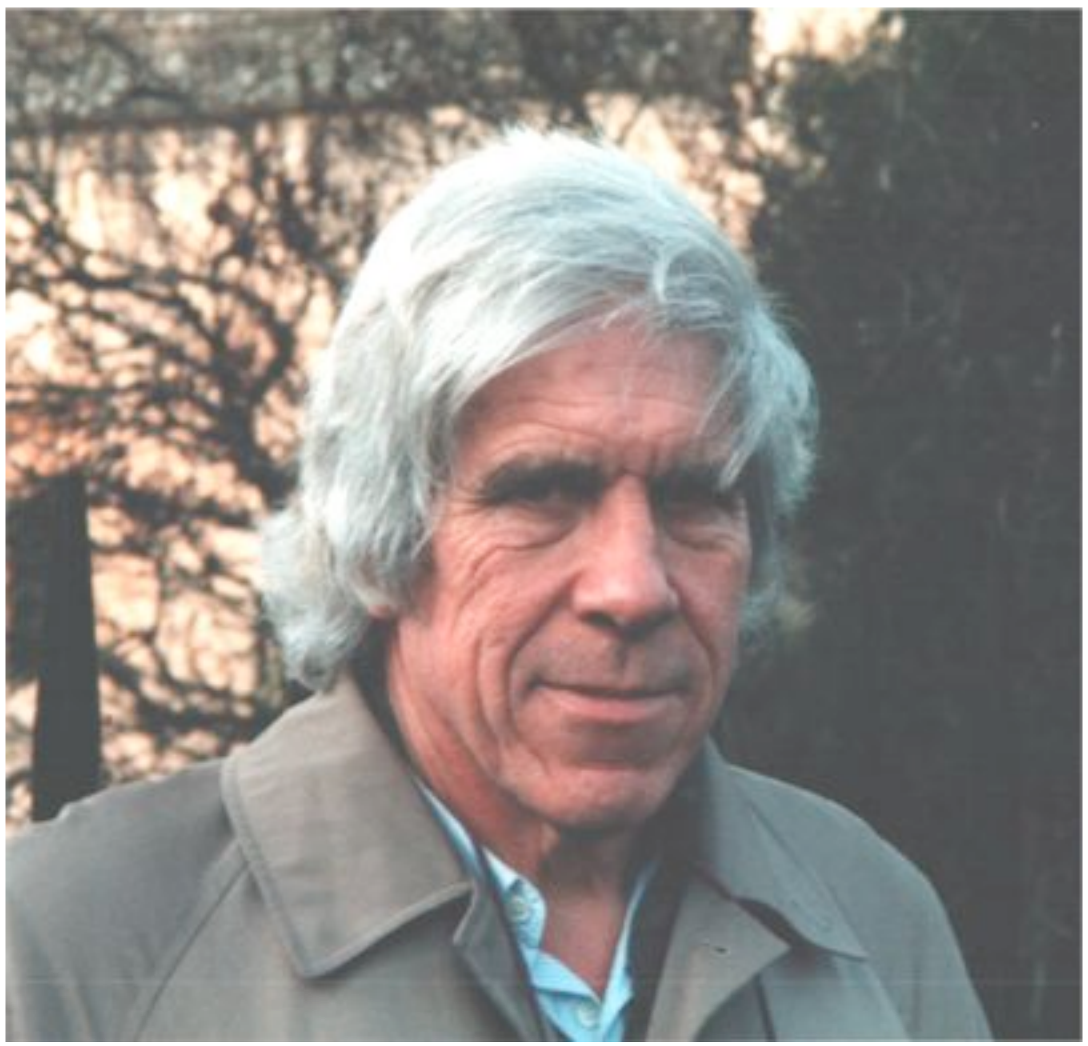
$\pi_i(\bullet, \bullet) = b/(n-1)$

$\pi_j(\bullet, \bullet) = -c$

$\pi_j({\color{blue}\bullet}, {\color{blue}\bullet}) = 0$

$$\boxed{\frac{dr_{i,A}}{dt} > 0 \Leftrightarrow \frac{b}{c} > 1 + \frac{n}{n_g} + \frac{\lambda}{q}}$$

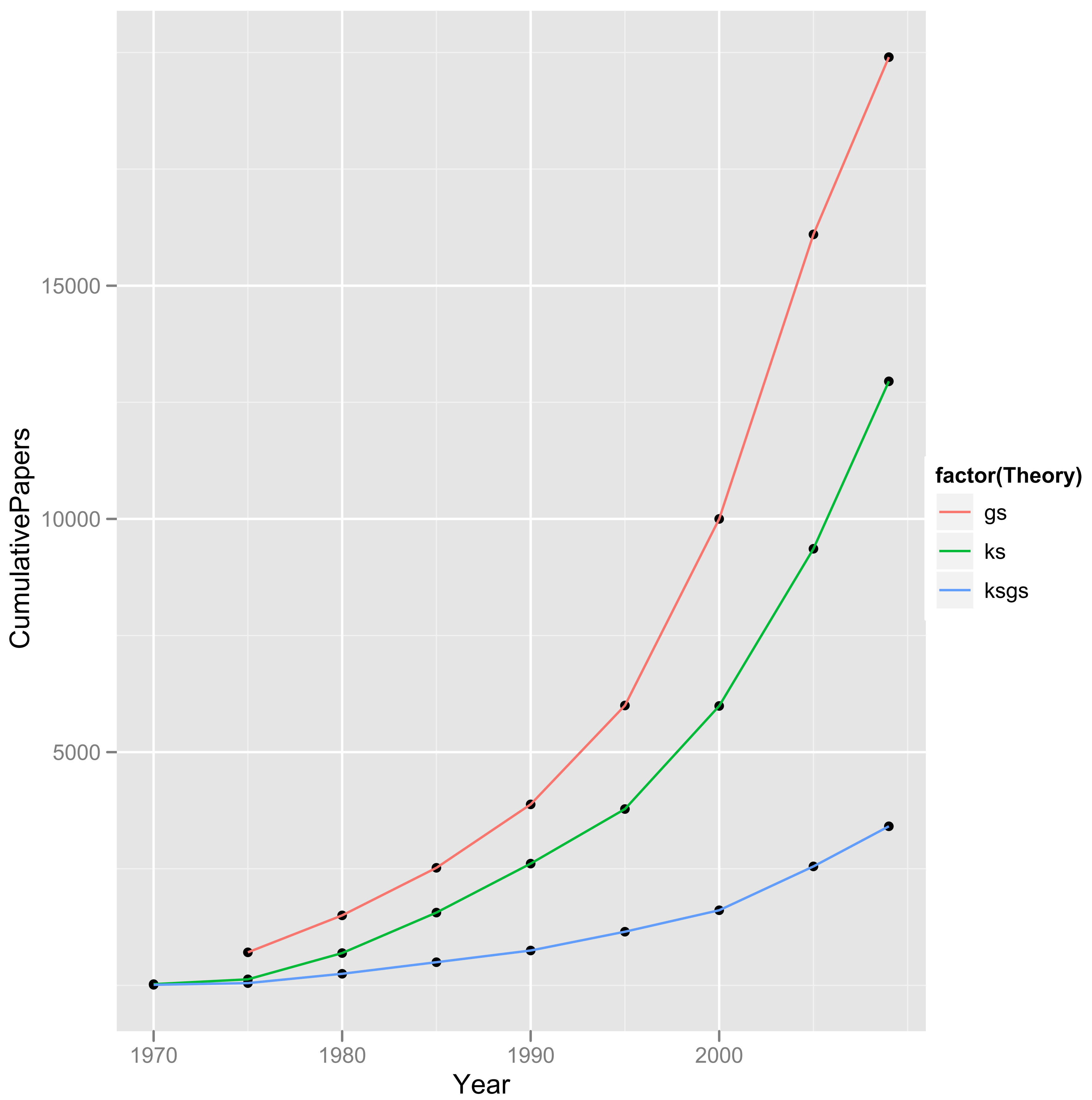
Kin/group Selection



William Hamilton

- $b/c > 1/r$
- r: probability that two genes are identical by sampling from ancestors

$$r \approx \frac{n_g}{n + n_g}$$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1970
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Year
factor(Theory)
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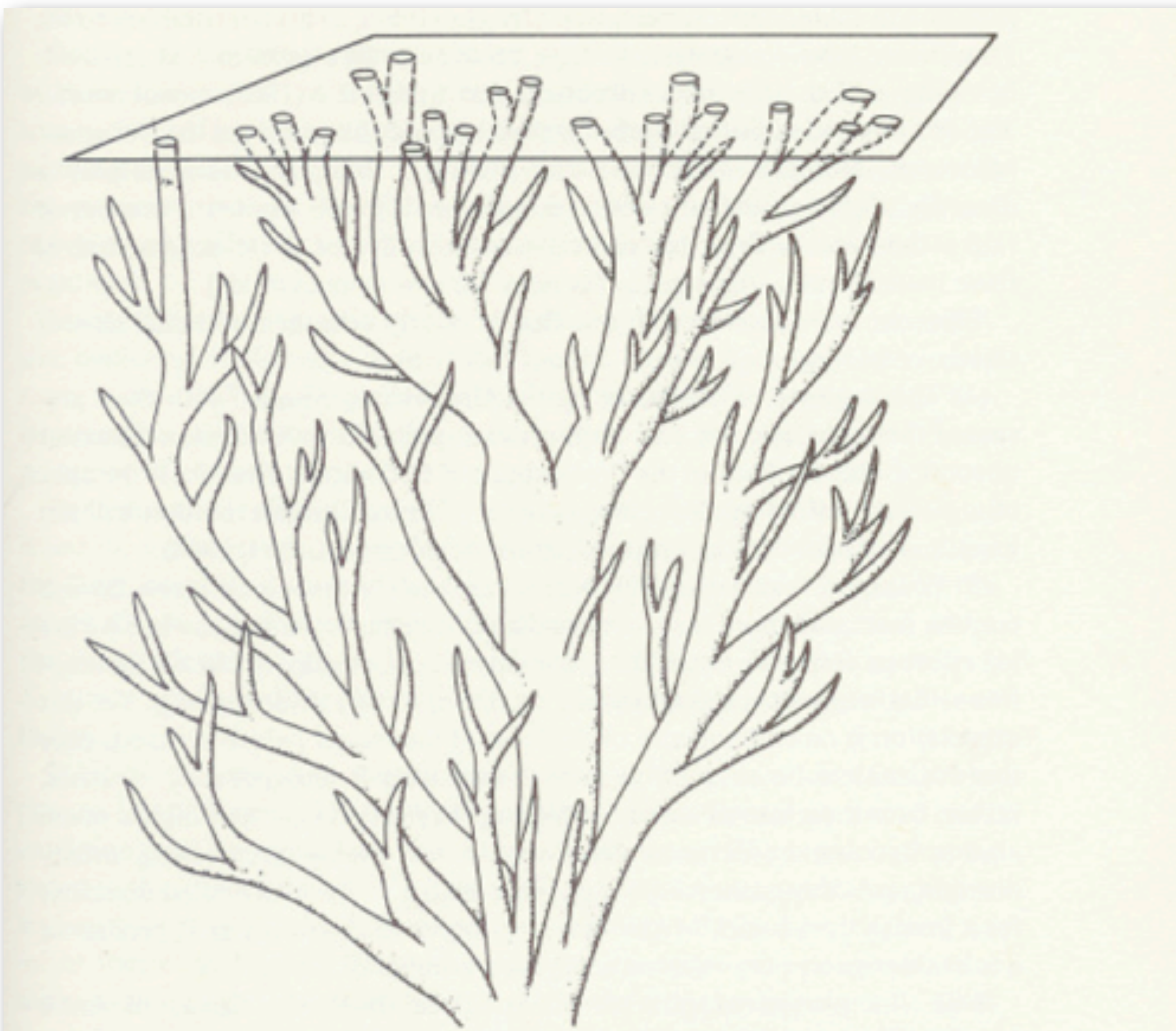
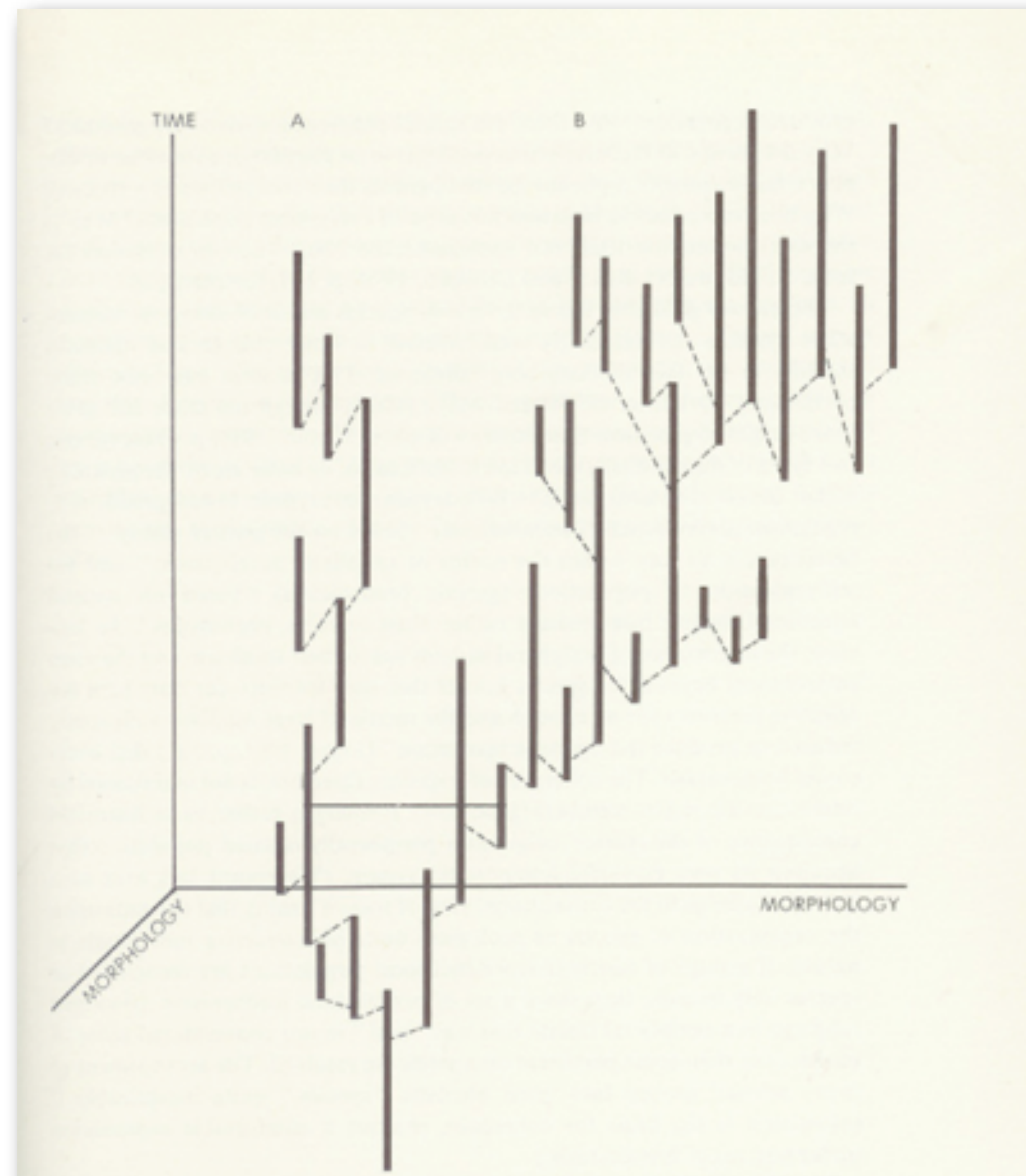
Micro versus Macro Evolution

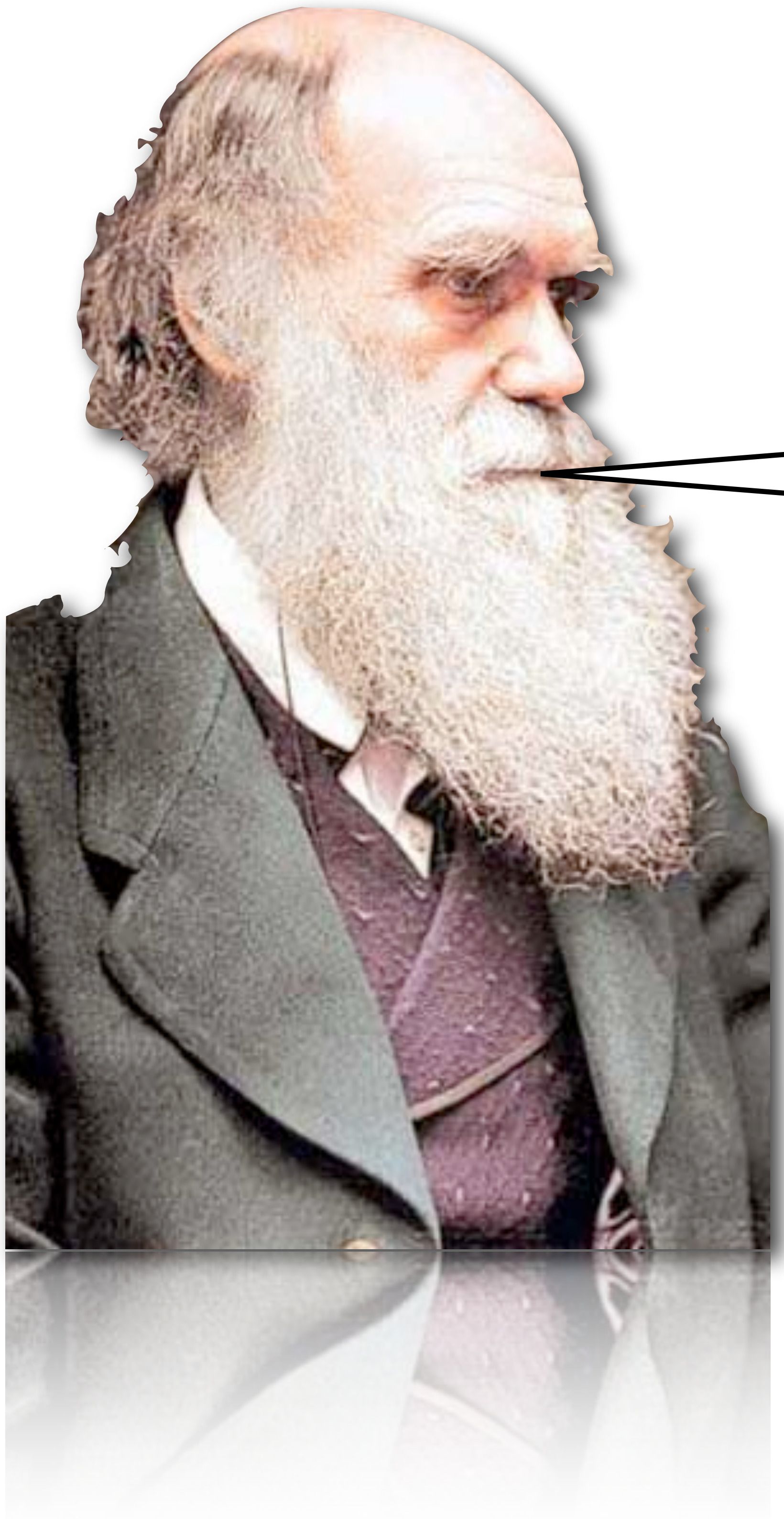
<u>Intuition</u> (1) - Macro is an average over Micro
<u>Intuition</u> (2) - Macro is distinct from Micro
<u>False Clue</u> - Pessimistic interpretation of Fossil Record
<u>Anomalous Observation</u> - Optimistic interpretation
<u>Techniques of Investigation</u> - Stochastic Processes/ Dynamical Systems/EvoDevo

An alternative to Phyletic Gradualism

Eldredge & Gould 1972







"Geology assuredly does not reveal any such finely-graduated organic chain; and **this, perhaps, is the most obvious and serious objection which can be urged against the theory**. The explanation lies, as I believe, in the extreme imperfection of the geological record." (1859)

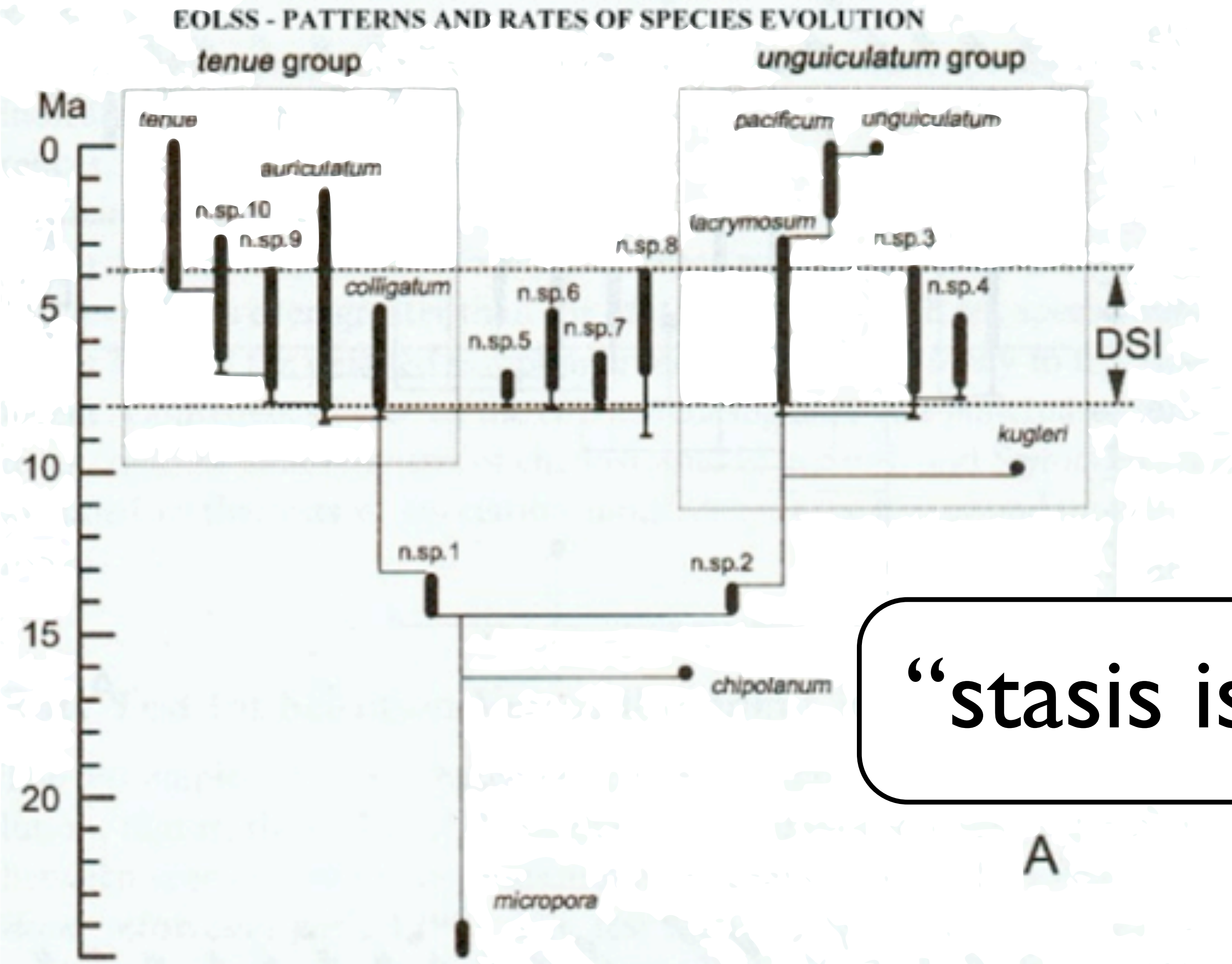
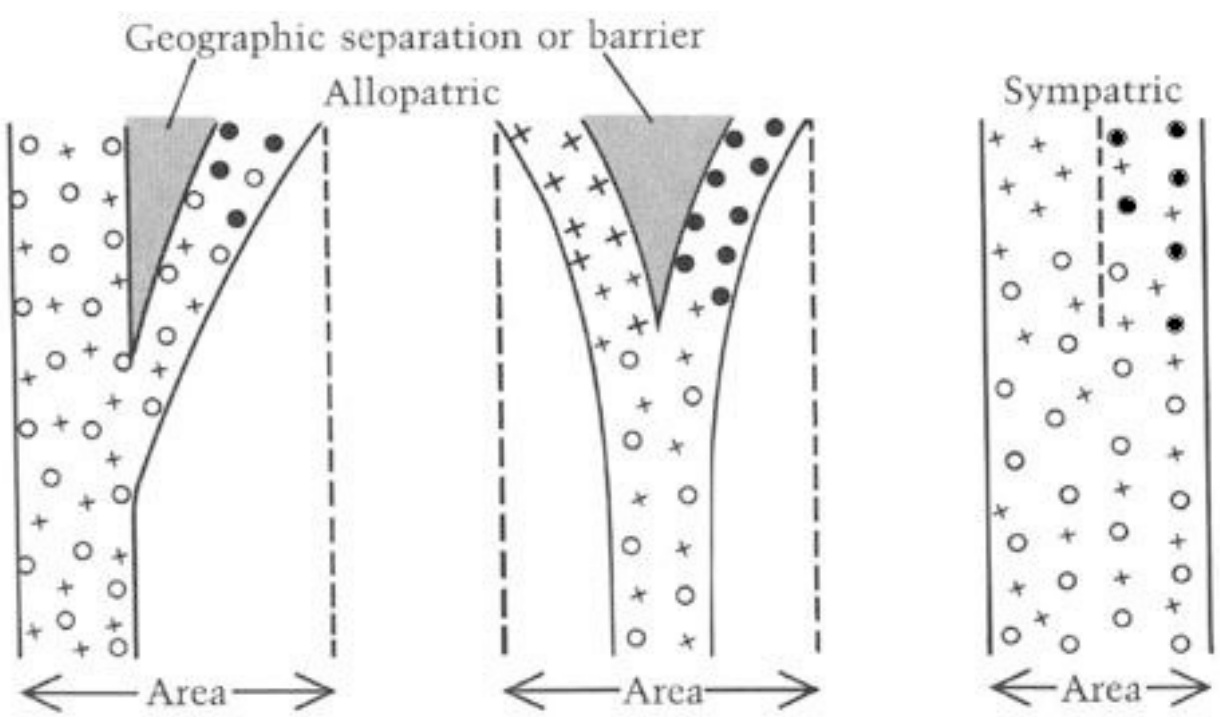
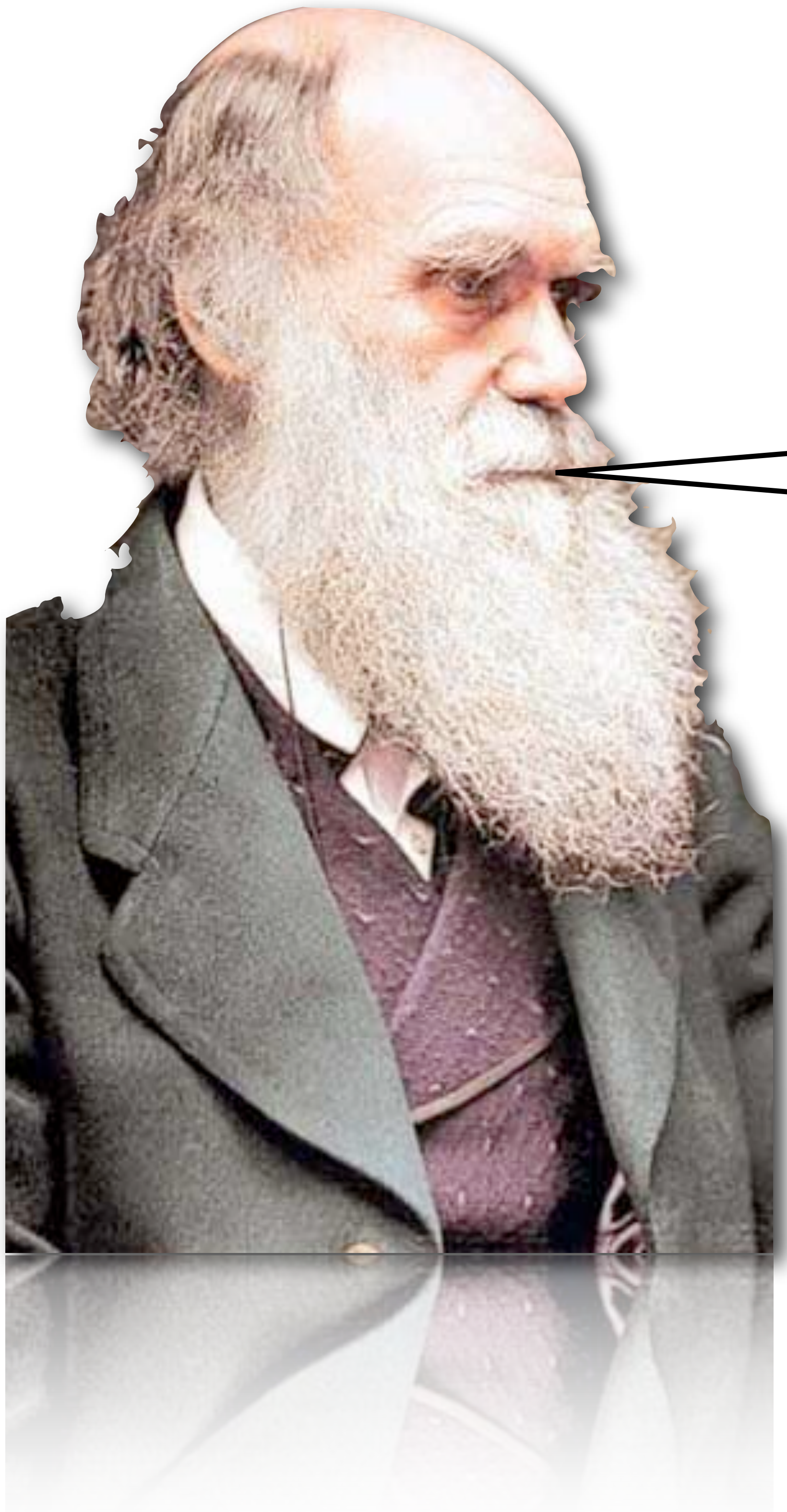


Fig. 6. Punctuational speciation in the bryozoan Metrarabdotos. The fossils show that Metrarabdotos radiated dramatically between 8 and 4 million years ago, and several species arose apparently rapidly, within the Dominican Sampling Interval (DSI), a particularly well sampled sequence. Based on the work of Cheetham and Jackson.

"stasis is data"

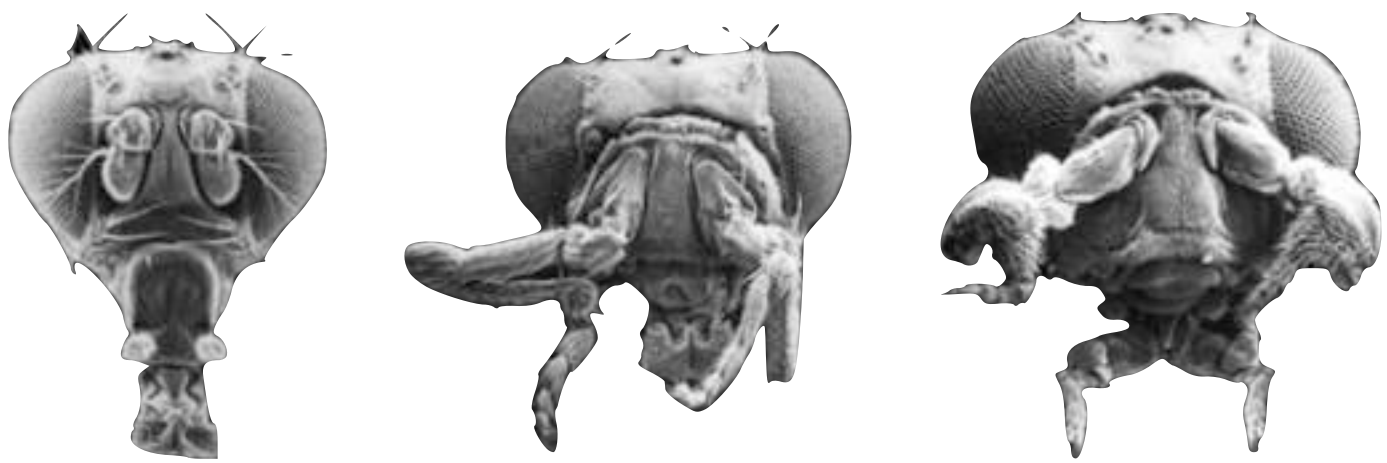
"but is this not what we expect?"

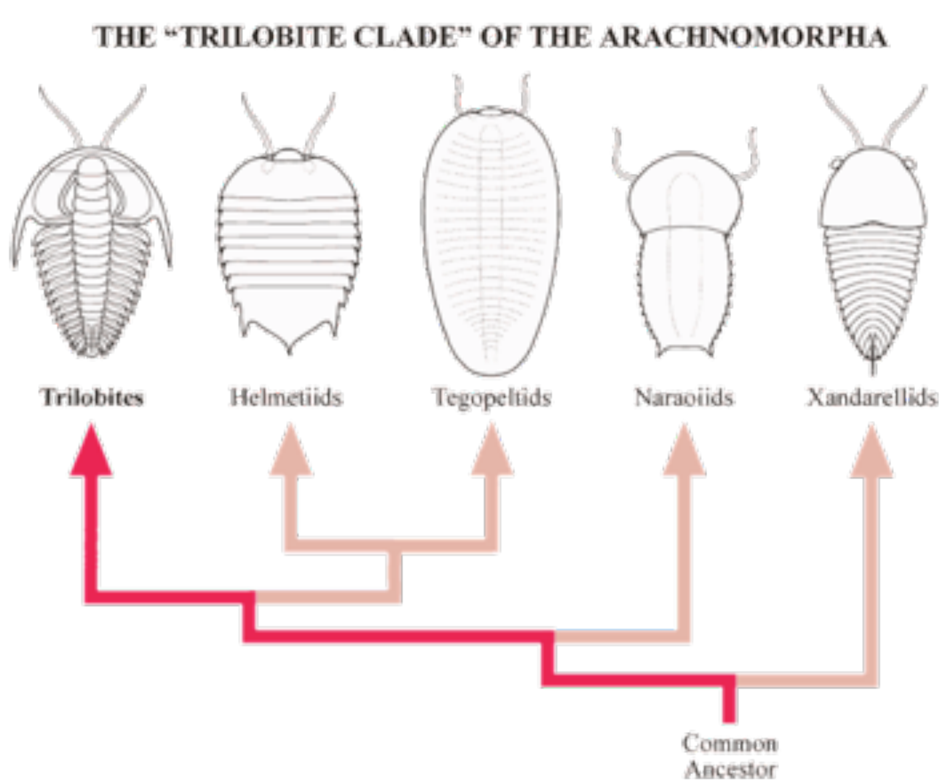


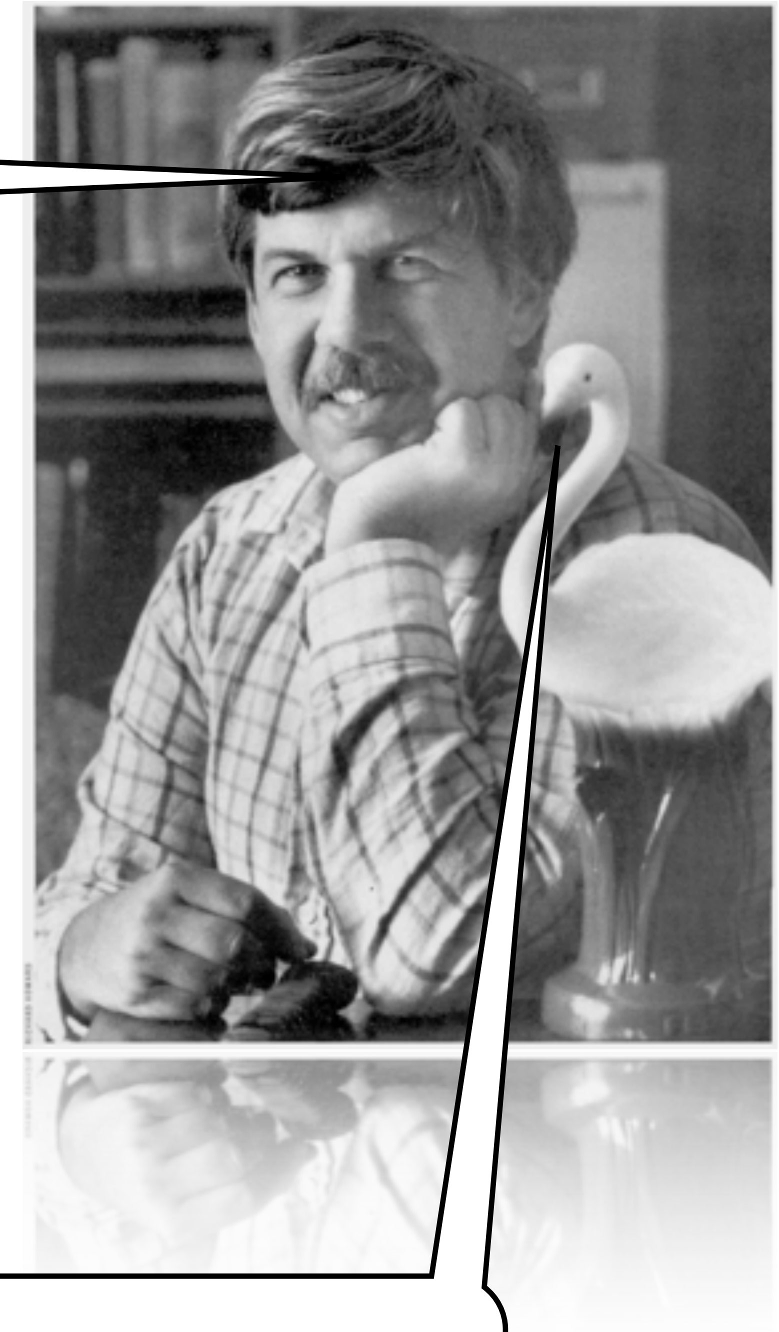


"...and lastly, although each species must have passed through numerous transitional stages, **it is probable that the periods, during which each underwent modification, though many and long as measured by years, have been short in comparison with the periods during which each remained in an unchanged condition**. ...He who rejects this view of the imperfection of the geological record, will rightly reject the whole theory. For he may ask in vain where are the numberless transitional links which must formerly have connected the closely allied or representative species, found in successive stages of the same great formation?" (1859)

Macroevolution is driven by macromutation & species selection





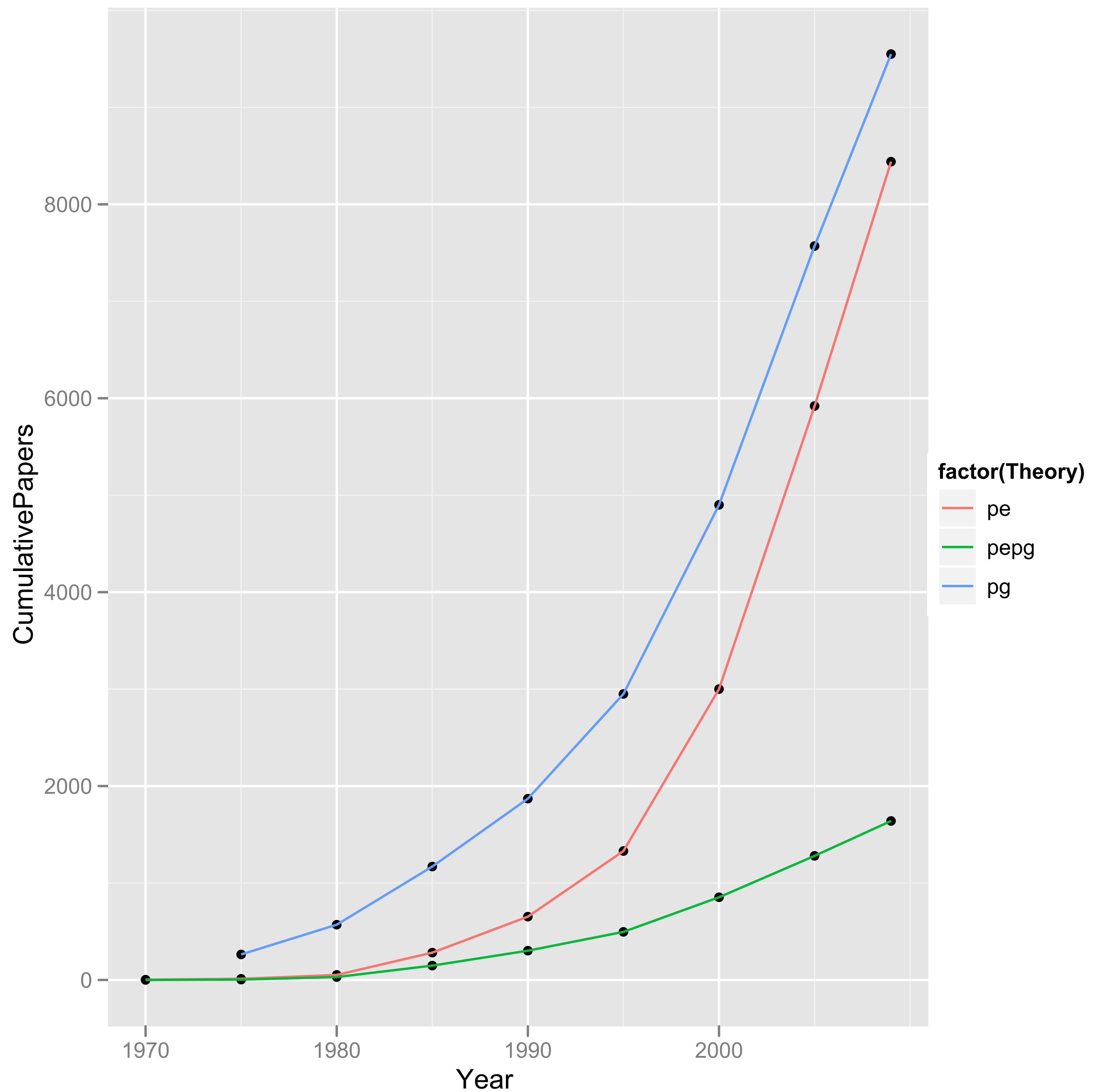


"That reminds me of Mendel & Bateson"

"Do you have any evidence?"

"there appears to be no basis for Davidson and Erwin's claim that the processes producing higher level clades differ from those creating lower level clades, or that different types of genetic change apply to different taxonomic levels"
Coyne (2006)

"different levels of change that have occurred in evolution are imperfectly reflected at different levels of Linnean classification," ... "these inhomogeneous events have been caused by architectural alterations in different locations in the underlying GRNs"
Davidson & Erwin (2006)


CumulativePapers
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Challenging the Foundations

Evo Devo

Niche Construction

Culture

Mind

appearance of dwarf and giant varieties	all
piebald coat color	all
wavy or curly hair	sheep, poodles, donkeys, horses, pigs goats, mice, guinea pigs
rolled tails	dogs, pigs
shortened tails, fewer vertebrae	dogs, cats, sheep
floppy ears	dogs, cats, pigs, horses, sheep, goats, cattle
changes in reproductive cycle	all except sheep

			increase in frequency (percent)
depigmentation (*Star*)	12,400	710	+1,646
brown mottling	450	86	+423
gray hairs	500	100	+400
floppy ears	230	170	+35
short tail	140	2	+6,900
tail rolled in circle	9,400	830	+1,033

From: L.N. Trut. Amer. Sci. (1999)

STRUCTURE AND DISTRIBUTION

OF

CORAL REEFS.

BEING THE FIRST PART OF
THE GEOLOGY OF THE VOYAGE OF THE BEAGLE,
UNDER THE COMMAND OF CAPT. FITZROY, R.N.

DURING THE YEARS 1832 TO 1836.

BY

CHARLES DARWIN, M.A., F.R.S., F.G.S.,
NATURALIST TO THE EXPEDITION.

Published with the Approval of the Lords Commissioners of
Her Majesty's Treasury.

LONDON:
SMITH, ELDER AND CO., 65, CORNHILL.

1842.

THE FORMATION

OF

VEGETABLE MOULD,

THROUGH THE

ACTION OF WORMS

WITH

OBSERVATIONS ON THEIR HABITS.

BY CHARLES DARWIN, LL.D., F.R.S.

WITH ILLUSTRATIONS.

SEVENTH THOUSAND (CORRECTED).

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1882.




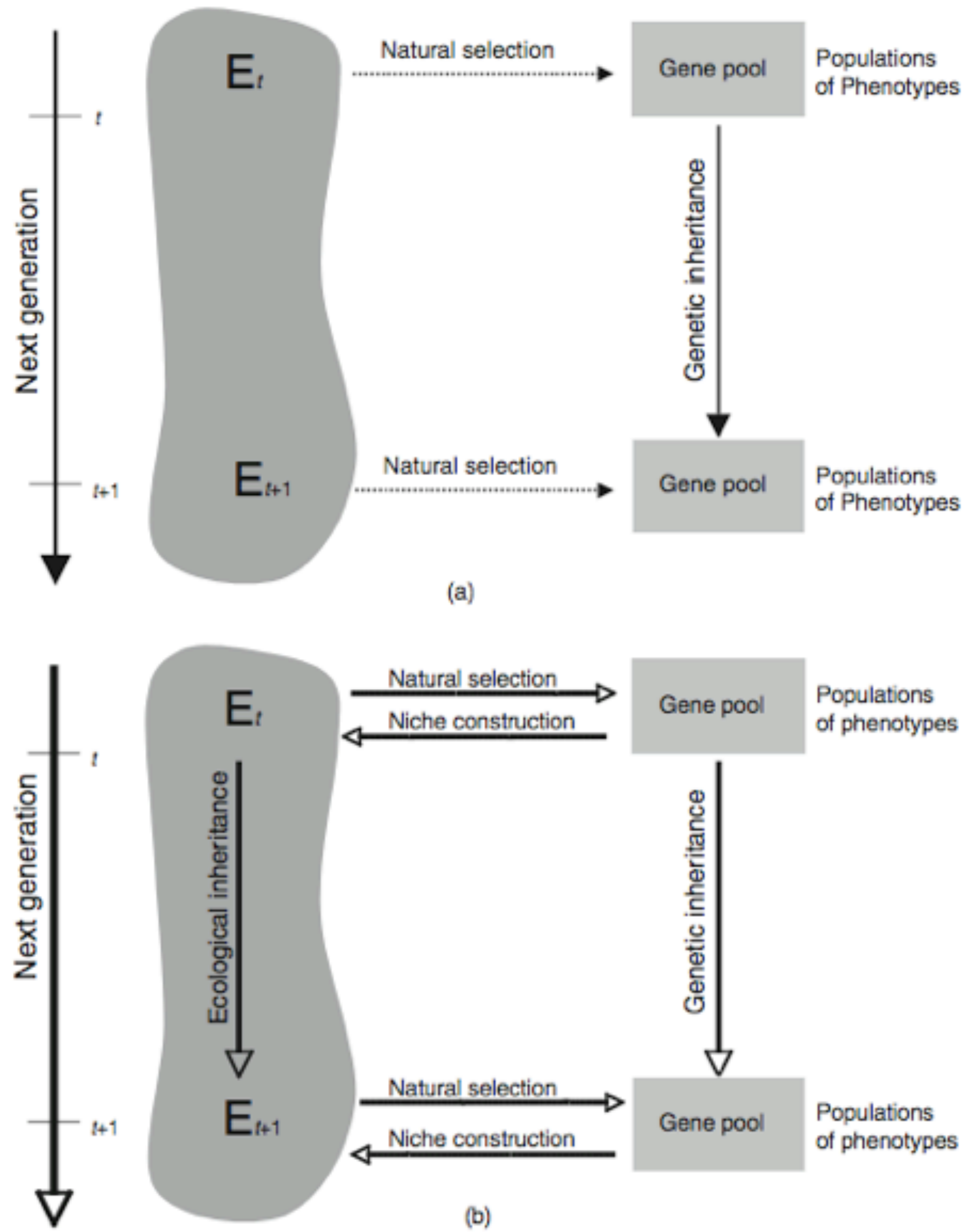

Figure 1.
a. Standard evolutionary theory. b. Extended evolutionary theory.

From: Odling Smee. Biol. Theor. 2007,
also see: Laland et al 2001, Krakauer et al 2009

OPEN ACCESS Freely available online PLoS COMPUTATIONAL BIOLOGY

An End to Endless Forms: Epistasis, Phenotype Distribution Bias, and Nonuniform Evolution

Elhanan Borenstein[1,2]*, **David C. Krakauer**[2]

1 Department of Biological Sciences, Stanford University, Stanford, California, United States of America, **2** Santa Fe Institute, Santa Fe, New Mexico, United States of America

Abstract

Studies of the evolution of development characterize the way in which gene regulatory dynamics during ontogeny constructs and channels phenotypic variation. These studies have identified a number of evolutionary regularities: (1) phenotypes occupy only a small subspace of possible phenotypes, (2) the influence of mutation is not uniform and is often canalized, and (3) a great deal of morphological variation evolved early in the history of multicellular life. An important implication of these studies is that diversity is largely the outcome of the evolution of gene regulation rather than the emergence of new, structural genes. Using a simple model that considers a generic property of developmental maps—the interaction between multiple genetic elements and the nonlinearity of gene interaction in shaping phenotypic traits—we are able to recover many of these empirical regularities. We show that visible phenotypes represent only a small fraction of possibilities. Epistasis ensures that phenotypes are highly clustered in morphospace and that the most frequent phenotypes are the most similar. We perform phylogenetic analyses on an evolving, developmental model and find that species become more alike through time, whereas higher-level grades have a tendency to diverge. Ancestral phenotypes, produced by early developmental programs with a low level of gene interaction, are found to span a significantly greater volume of the total phenotypic space than derived taxa. We suggest that early and late evolution have a different character that we classify into micro- and macroevolutionary configurations. These findings complement the view of development as a key component in the production of endless forms and highlight the crucial role of development in constraining biotic diversity and evolutionary trajectories.

Citation: Borenstein E, Krakauer DC (2008) An End to Endless Forms: Epistasis, Phenotype Distribution Bias, and Nonuniform Evolution. PLoS Comput Biol 4(10): e1000202. doi:10.1371/journal.pcbi.1000202

Borenstein & Krakauer, 2009

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Diversity, Dilemmas, and Monopolies of Niche Construction

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3. Department of Paleobiology, MRC-121, National Museum of Natural History, Washington, DC 20013

Submitted January 29, 2008; Accepted May 30, 2008; Electronically published December 5, 2008

Online enhancements: appendixes.

Niche Construction and Ecological Monopolies

A multitude of selection processes impinge on organisms, modifying their replication rates, death rates, and population densities. Through evolutionary time, species have increased their control over environmental feedback to increase or stabilize their abundance. The acquisition of such adaptations may also increase the diversity of these clades through time. There are, broadly speaking, two strategies available to achieve increased environmental control. One is to reduce the dependence of organisms on environmental factors by increasing the number of traits that insulate them from uncertainties in the environment.

Krakauer, Page & Erwin 2008

Contents lists available at ScienceDirect

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journal homepage: www.elsevier.com/locate/yjtbi

ELSEVIER

Developmental autonomy and somatic niche construction promotes robust cell fate decisions

Anya K. Bershad[a,b,c], Miguel A. Fuentes[c,d], David C. Krakauer[c,*]

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[c] *Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA*
[d] *Centro Atómico Bariloche, Instituto Balseiro and CONICET, 8400 Bariloche, Argentina*

Bershad, Fuentes & Krakauer 2008

The Future (or at least the next lecture):
Evolution and Cognition

Art -- math -- Slides

Replicator Equation

n genomes

$$\dot{g}_i = g_i(r_i - \bar{f})$$

where $\bar{f} = \sum_i^n r_i g_i$ and $c_{ij} = 1$

Game Dynamical Eq.

$$\dot{g}_i = g_i(r_i(\mathbf{g}) - \bar{f})$$

$$\text{Payoff Matrix } \; P = [p_{ij}]$$

with linear payoffs:

$$r_i(\mathbf{g}) = \sum_j^n g_j p_{ij}$$

Replicator-Mutator Equation

$$\dot{g}_i = \sum_{j}^{2^n} g_j r_j(\mathbf{g}) m_{ij} - g_i \bar{f}$$

$$m_{ij} = \mu^{H(i,j)}(1-\mu)^{L-H(i,j)}$$

The Price Equation

$$\dot{E}[p] = Cov(r, p) + E[\dot{p}] + E[r\Delta_m p]$$

Adaptive Dynamics Eq.

$$\frac{dx}{dt} = \frac{1}{2}\mu\sigma^2\bar{N}(x)\frac{\delta f(x',x)}{\delta x'}\bigg|_{x'=x}$$

A few References

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