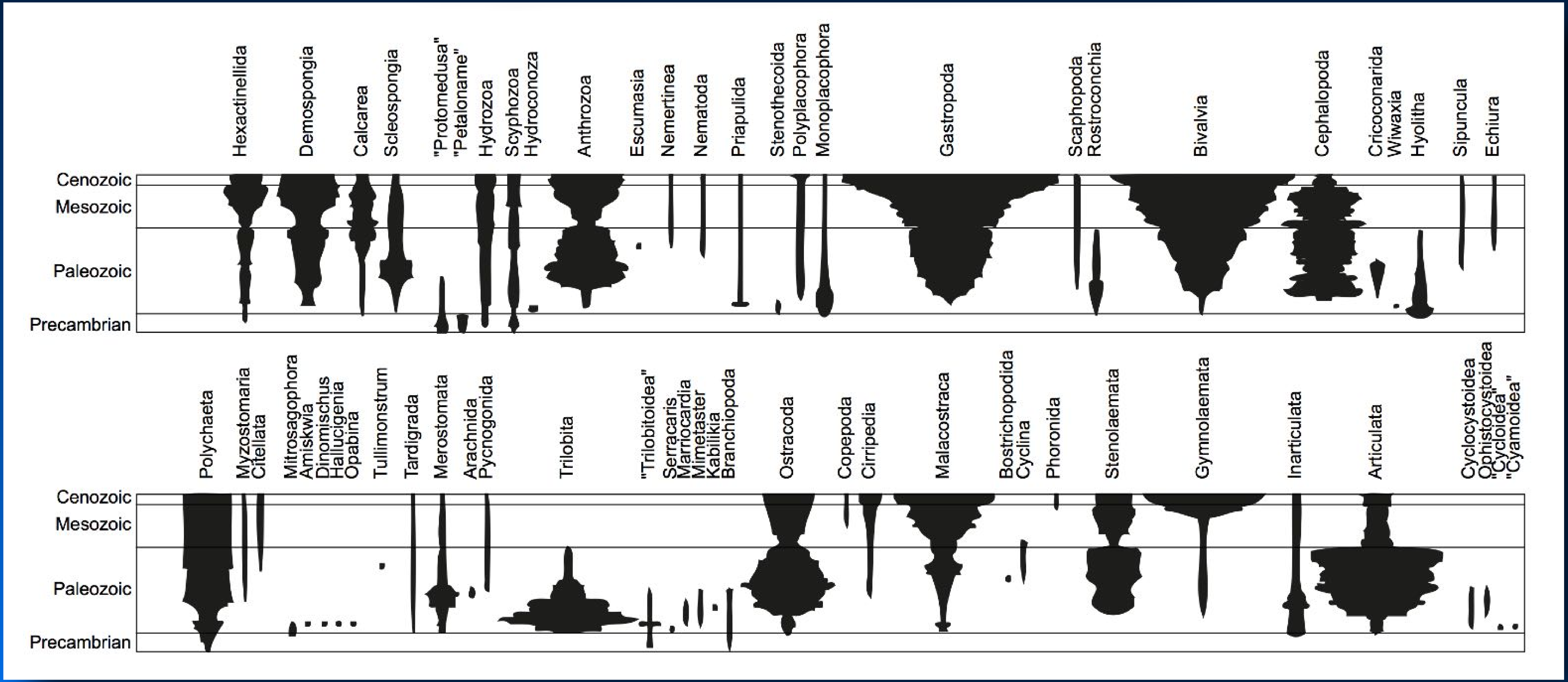
NJU Course

# Principles of Paleobiology

## Tempos & Modes of Macroevolution

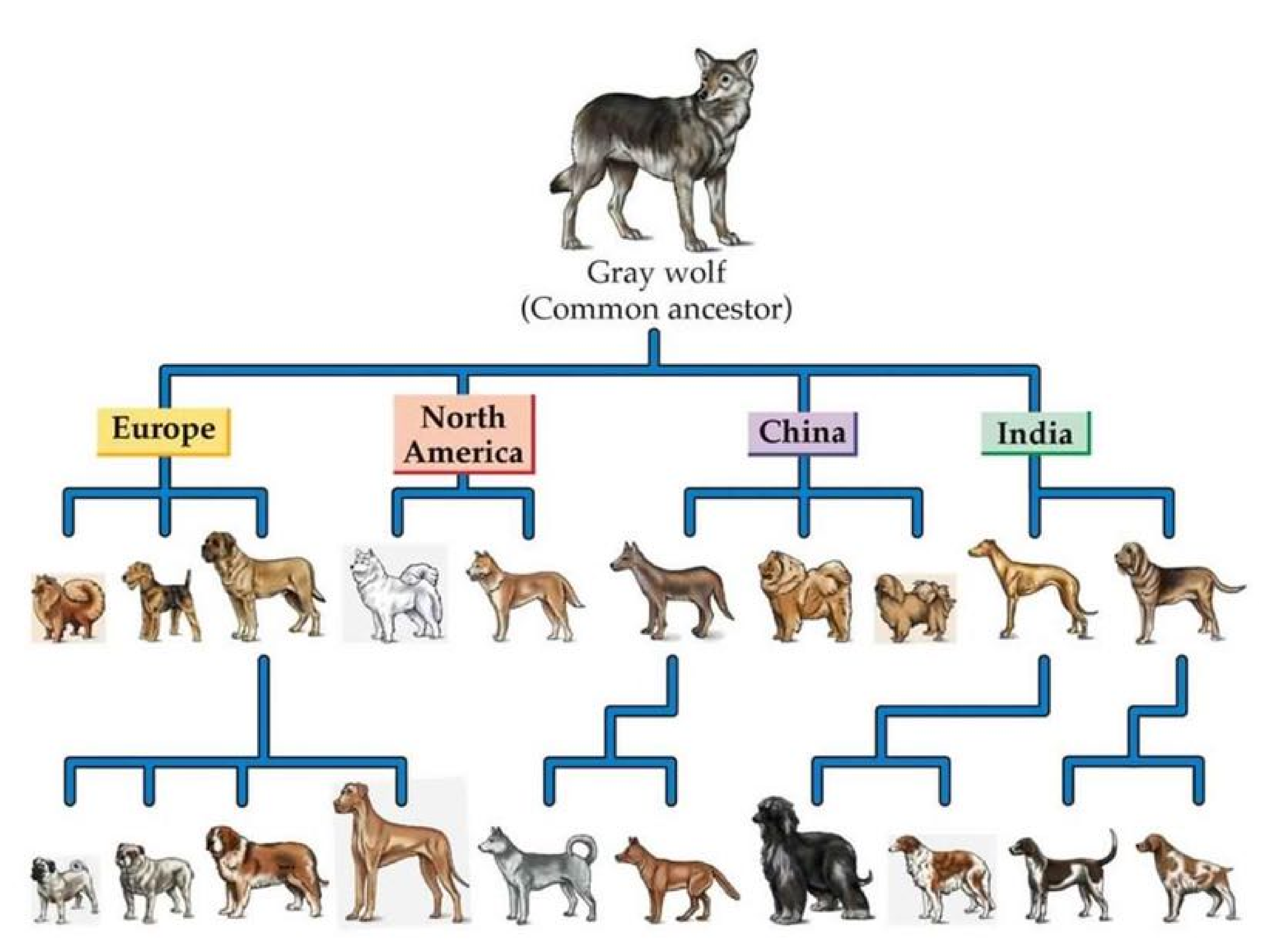


# Tempos & Modes of Macroevolution

## Microevolution

Heritable changes in allele frequencies within a population that occur over relatively short time intervals in response to infraspecific selection.

Microevolution is the type evolution Darwin proposed and the type that stands at the heart of the most widely accepted contemporary theory of evolution. While genetic allele frequencies can change over relatively short time intervals, enormously long time intervals are required to make large phenotypic changes. Indeed, among the primary initial objections to Darwin's theory was that earth history (as it was then known) provided insufficient time for microevolutionary processes to produce modern levels of phenotypic diversity.

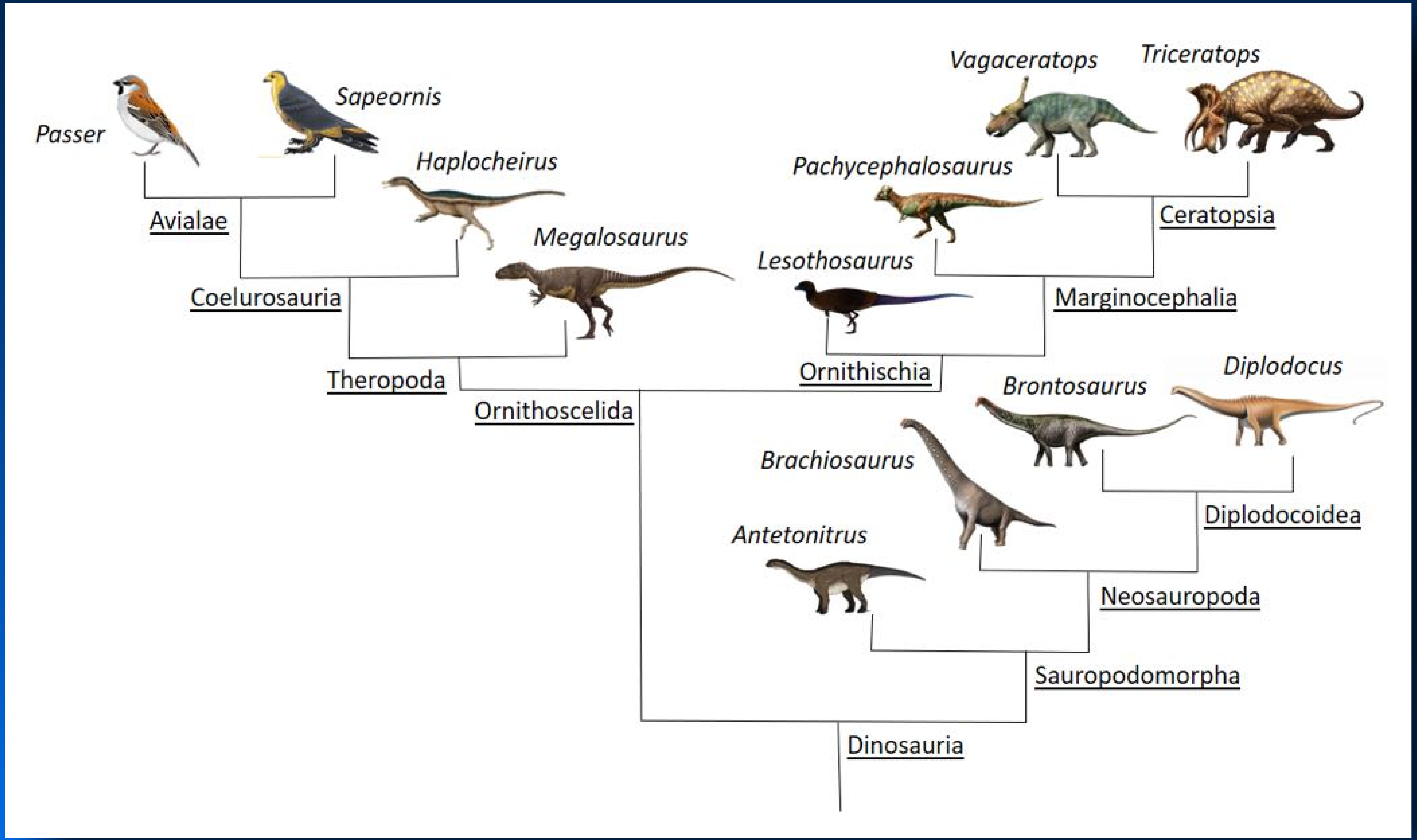


# Tempos & Modes of Macroevolution

## Macroevolution

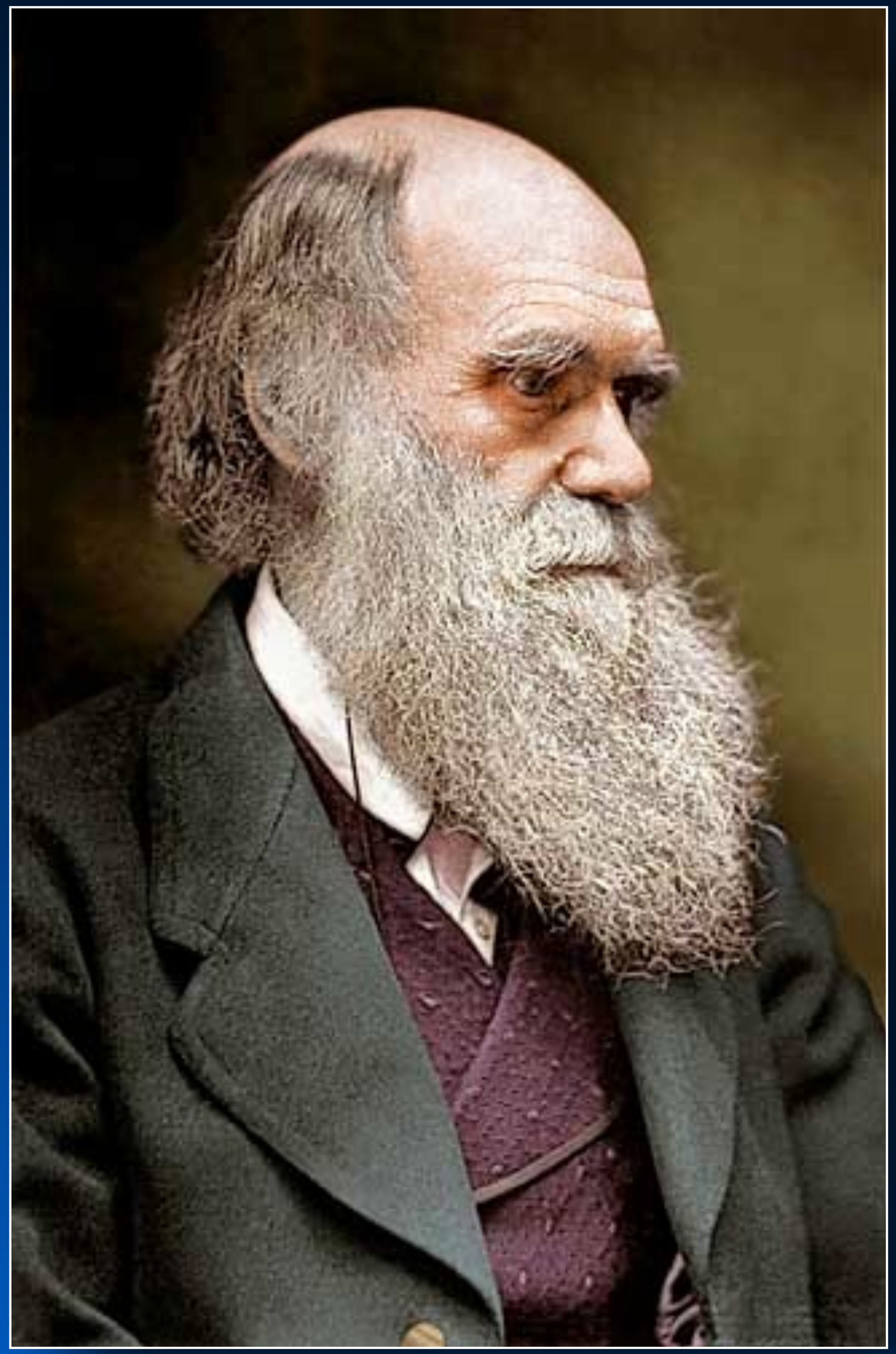
Changes in species composition within a lineage that occur over relatively long time intervals in response to interspecific selection.

Macroevolution began as a reaction to Darwin's theory that was consistent with short time frames and a literal reading of the fossil record. It was also though originally be more consistent with Mendelian genetics than micro-evolution. However, as more information became available these inconsistencies faded. Yet interest in macroevolutionary patterns and processes remains strong. Many believe it is an aspect of evolution yet to be understood fully.



# Tempos & Modes of Macroevolution

## Gradualism



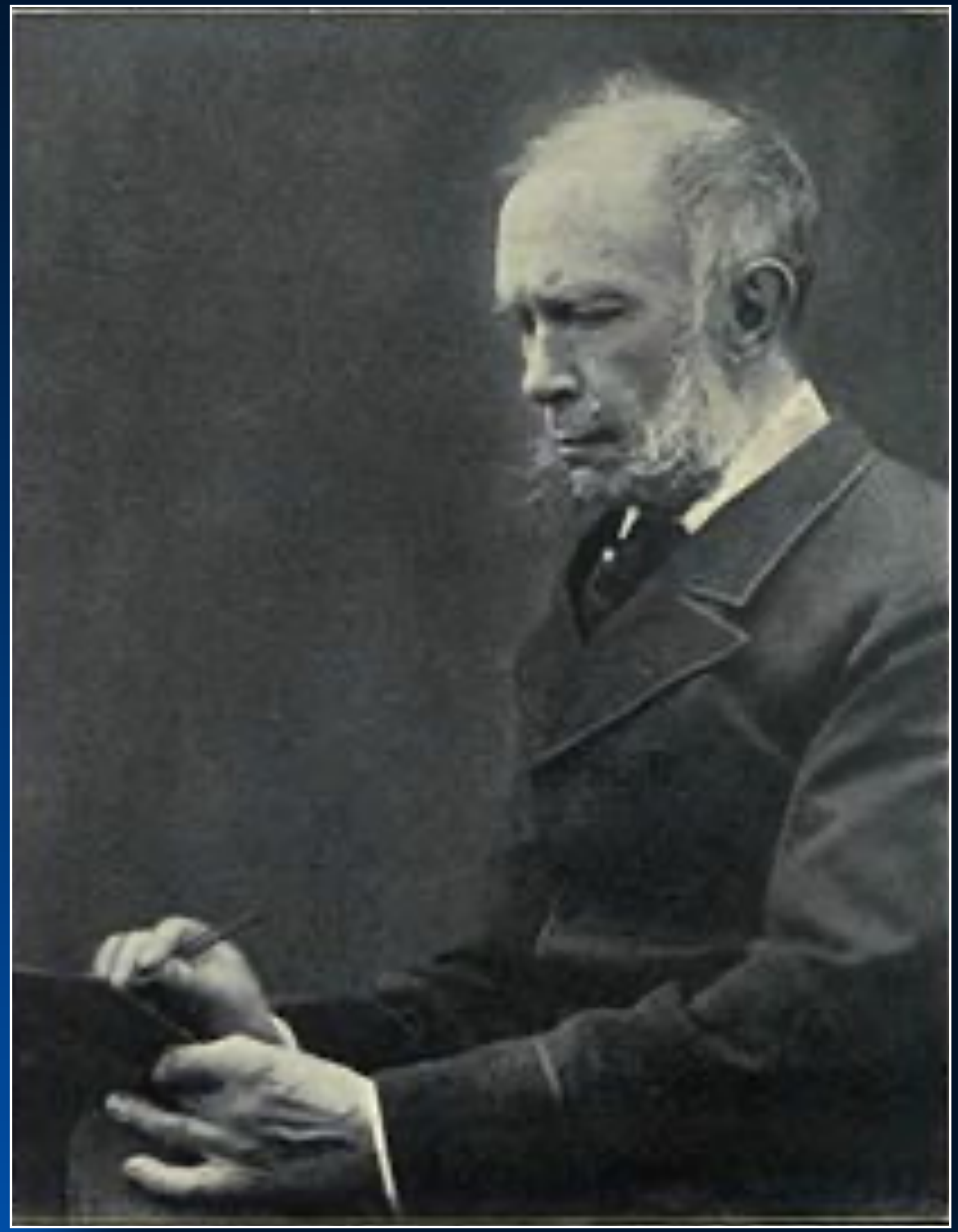
Charles Darwin
(1809 – 1882)

Darwin's concept of evolution was founded in the idea that natural selection operated on very small differences in the phenotypes of populations with better adapted individuals producing marginally more offspring than their less well-adapted neighbors. This idea was derived from Charles Lyell's view of geological change and relegated speciation to be a gradual divergence of morphological traits within a population over long intervals of time.

However, in order for this model to be reasonable it must be assumed that selection pressure remains uni-directional and constant over the time interval required for speciation to be completed; which may be thousands to millions of years. In this context Darin regarded the absence of transitional forms in the geological record as the strongest argument against his theory.

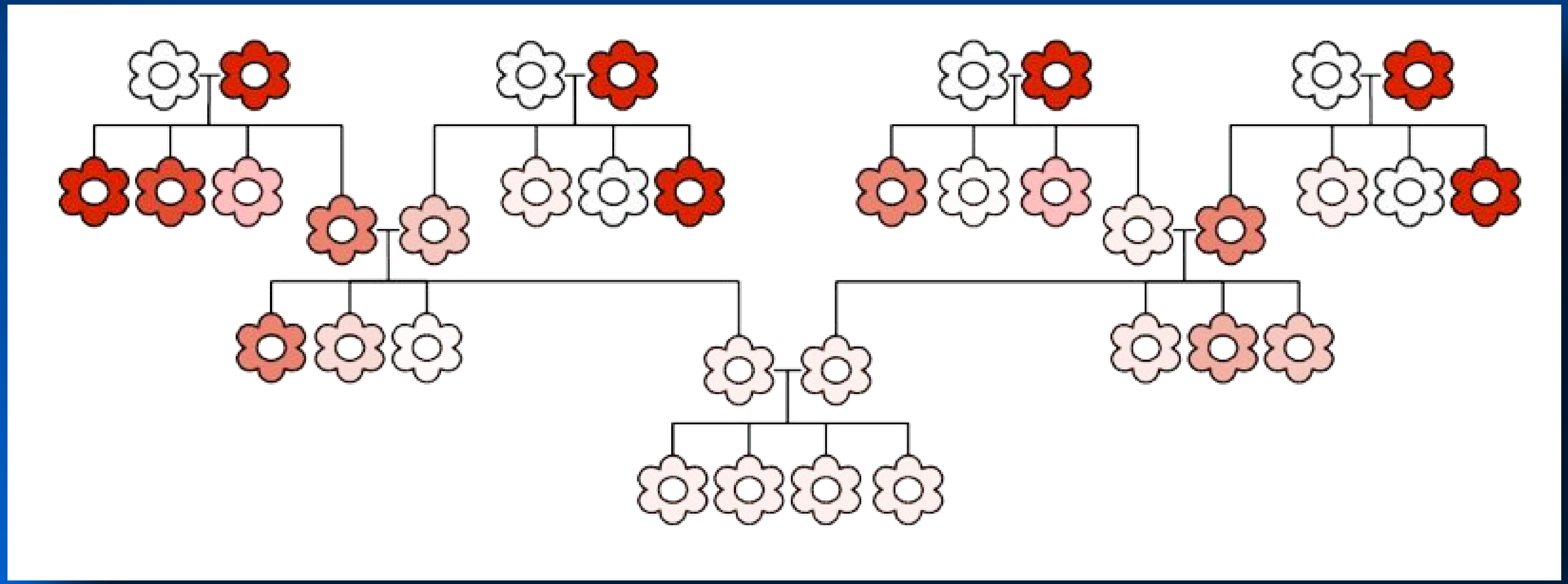
# Tempos & Modes of Macroevolution

## Blending Inheritance



Fleeming Jenkin
(1833 – 1885)

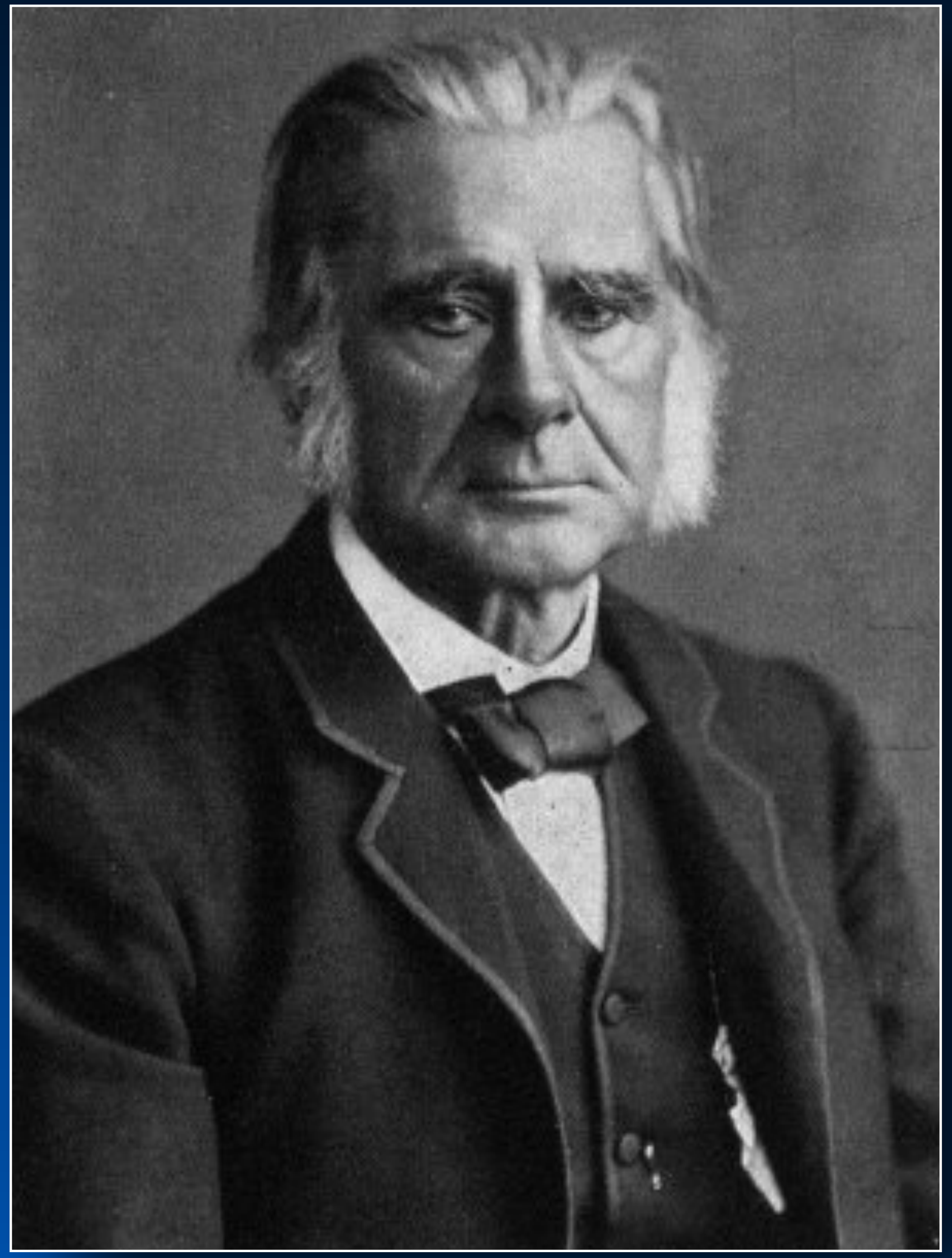
British engineer (inventor of the cable car), economist, linguist, critic, actor and artist. Jenkin published a powerful criticism of Darwin's evolutionary theory by proving mathematically that, under Darwin's model of blending inheritance (= offspring inherit the average of the parents phenotypic traits), any advantageous trait would be blended out of a population in just a few generations.



Ultimately blending inheritance was rejected by evolutionists in favor of Mendel's particulate inheritance model.

# Tempos & Modes of Macroevolution

## Saltationism



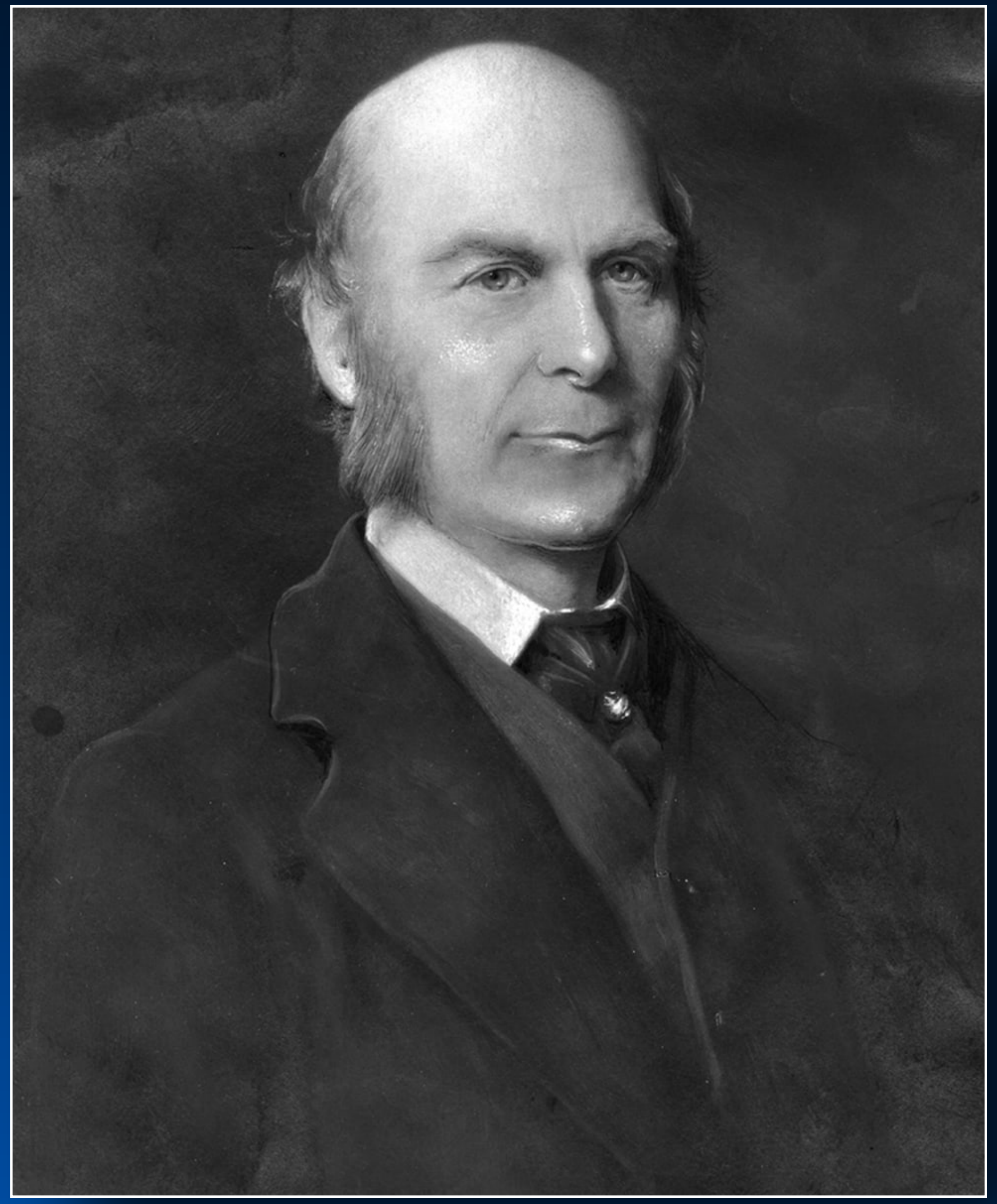
Thomas Henry Huxley
(1825 – 1895)

Thomas Henry Huxley was among those who accepted Darwin's theory of natural selection, but dissented from the idea that all evolutionary change had to be gradual. Huxley (and others) pointed to the absence of transitional forms in the geological record and argued that this supported the idea that natural selection does not operate primarily on individual differences among members of a population. Rather, it operates on the discontinuous differences observed among species.

Huxley went on to argue that these discontinuities are not by-products of an incomplete fossil record. Rather they are factual statements regarding how variation in natural world is produced and structured. Most importantly, Huxley (and others) believed these discontinuities — or "saltations" — arose suddenly at speciation events rather then gradually over long time intervals. This model of evolutionary change avoided Jenkin's criticisms of blended inheritance.

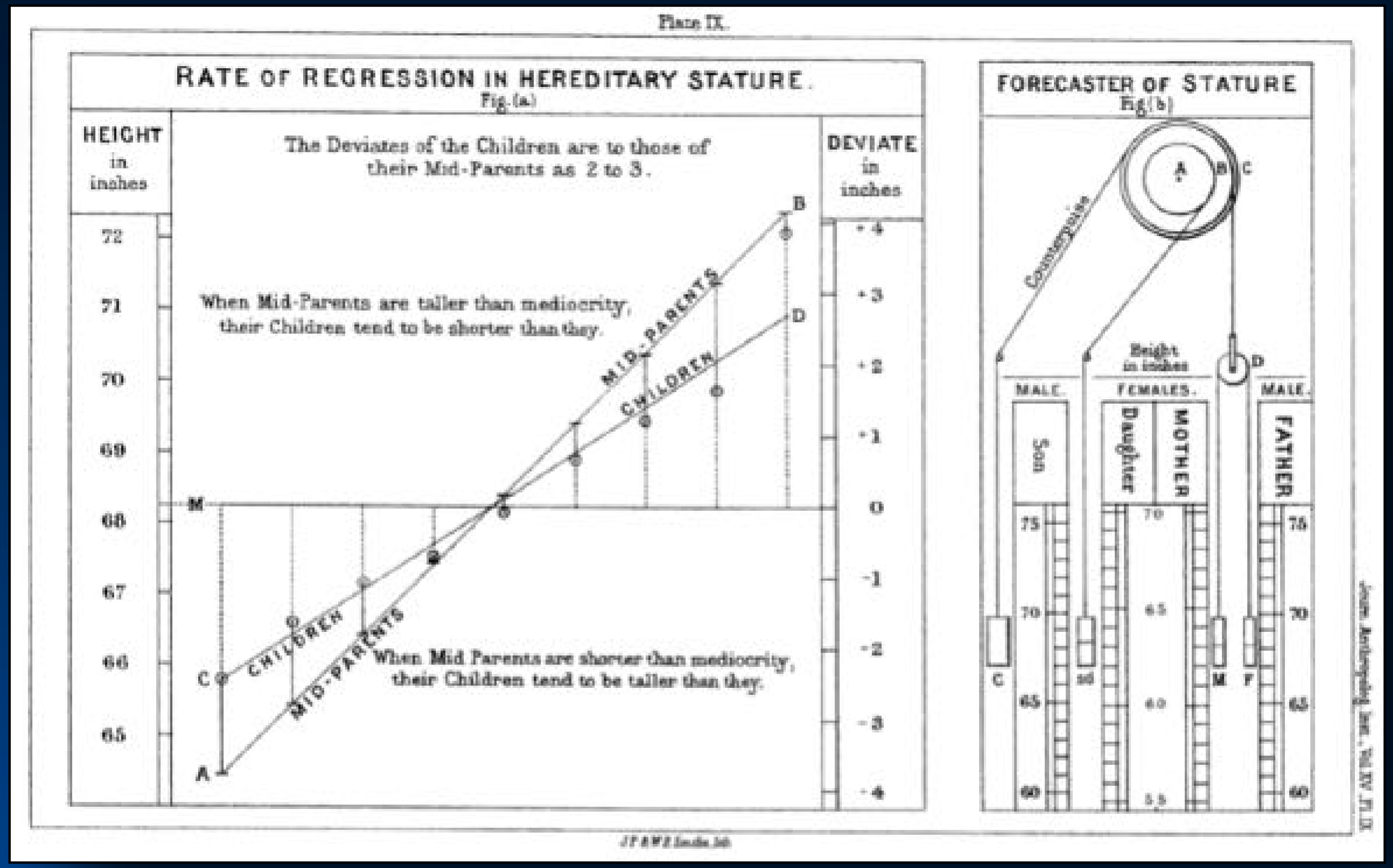
# Tempos & Modes of Macroevolution

## Biometry



Francis Galton
(1822 – 1911)

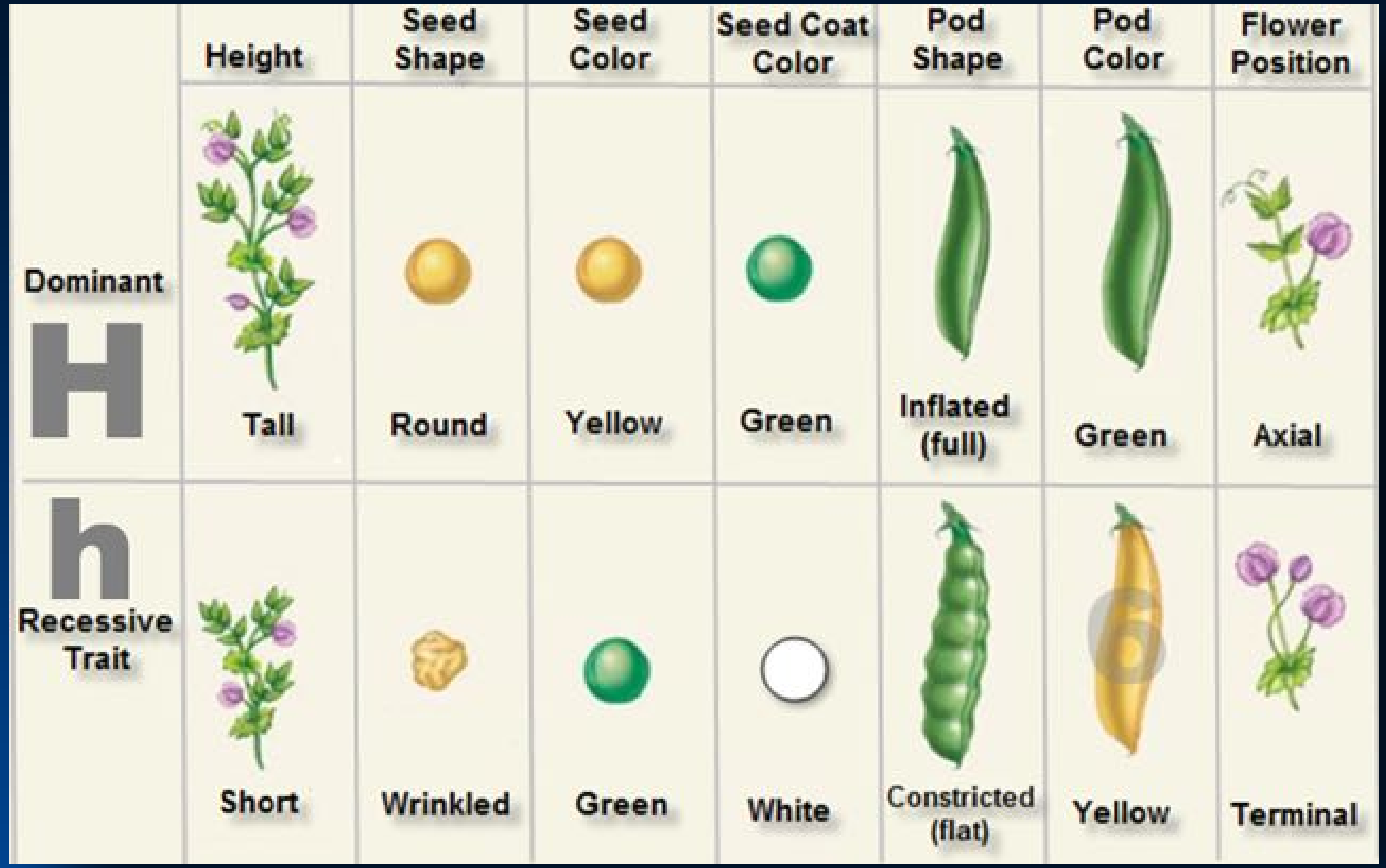
British polymath, founder of biometry and cousin of Charles Darwin. Galton invented linear regression analysis to test Darwin's theory of natural selection in light of Jenkin's argument.

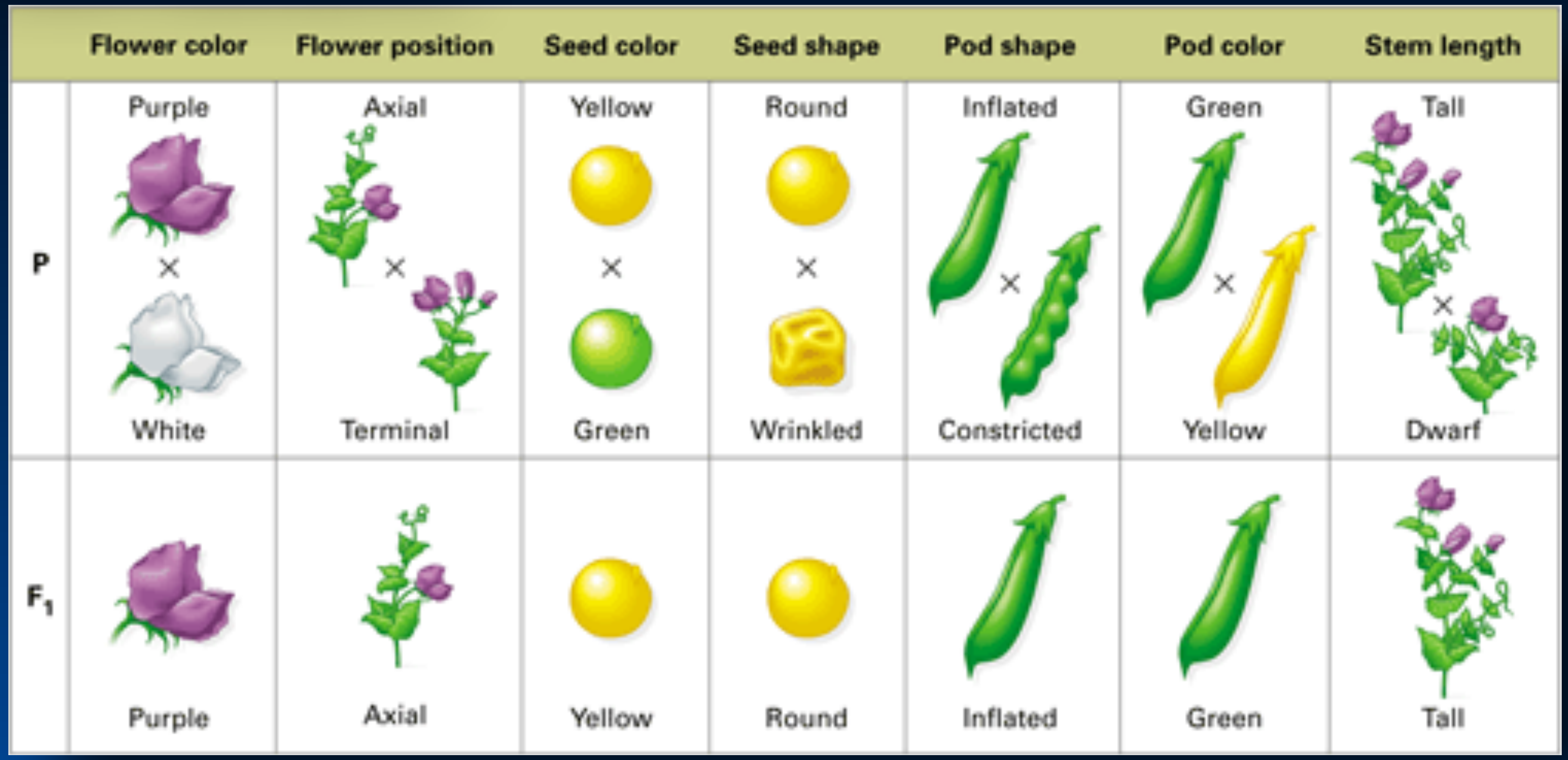



Based on his results Galton concluded that, whatever the mechanism of inheritance was, it was highly unlikely that random matings could produce offspring that transcended the original population's range of variation, because even mating between exceptional individuals displayed a tendency to produce offspring that exhibited characteristics closer to the population mean than those of the parents. Galton termed this tendency "regression" toward the mean.

# Tempos & Modes of Macroevolution

## The Mendelians




Mendel showed that genes occur in two varieties or alleles — dominant and recessive — and are passed from parents to offspring as paired units or particles. Homozygous pairings breed true, but heterozygous pairings adopt the form of the dominant allele.

In his study Mendel chose seven characteristics that were determined by single genes with two alleles. This meant he could trace, and confirm, the pattern of inheritance with precision. But his results left the Mendelians with the impression that genes can produce radical changes in the phenotype with no intermediates.

# Tempos & Modes of Macroevolution

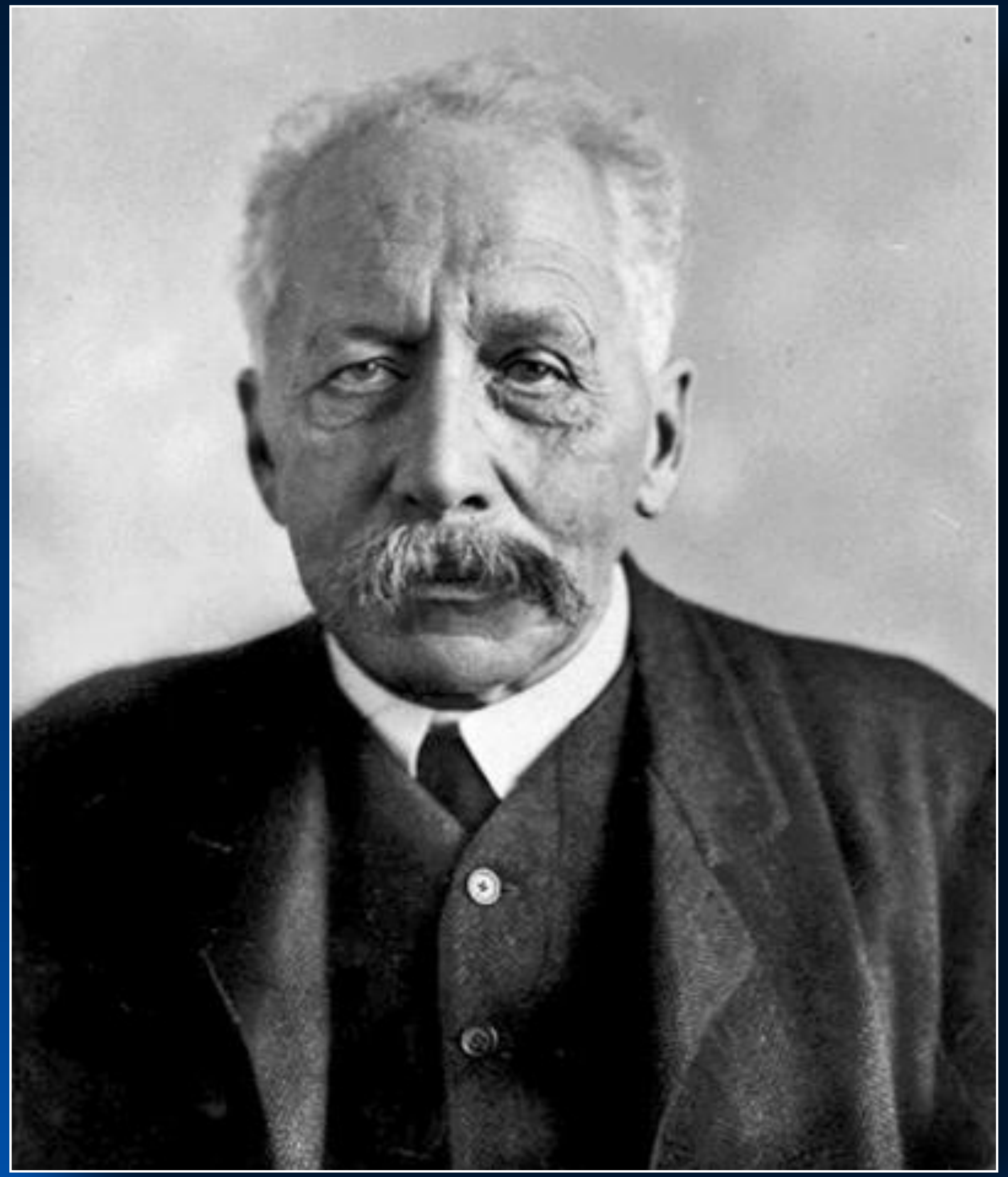
## The Biometricians

Pearson examined values of the correlation coefficient between fraternal siblings (fraternal correlation) with the correlation coefficient calculated between different “undifferentiated organs “ (e.g., flower petals, tree leaves, fish scales) belonging to the same individual. Unexpectedly, he discovered that, in a wide variety of cases, these values were similar (c. $r = 0.45$).

Pearson concluded that variation due to heredity (e.g., parents and offspring) was identical to the magnitude of variation observed within individual organisms (= quite modest). The modest magnitude of this variation accorded well with Darwin’s statements regarding his expectations of gradual and progressive variation between generations of a single population.

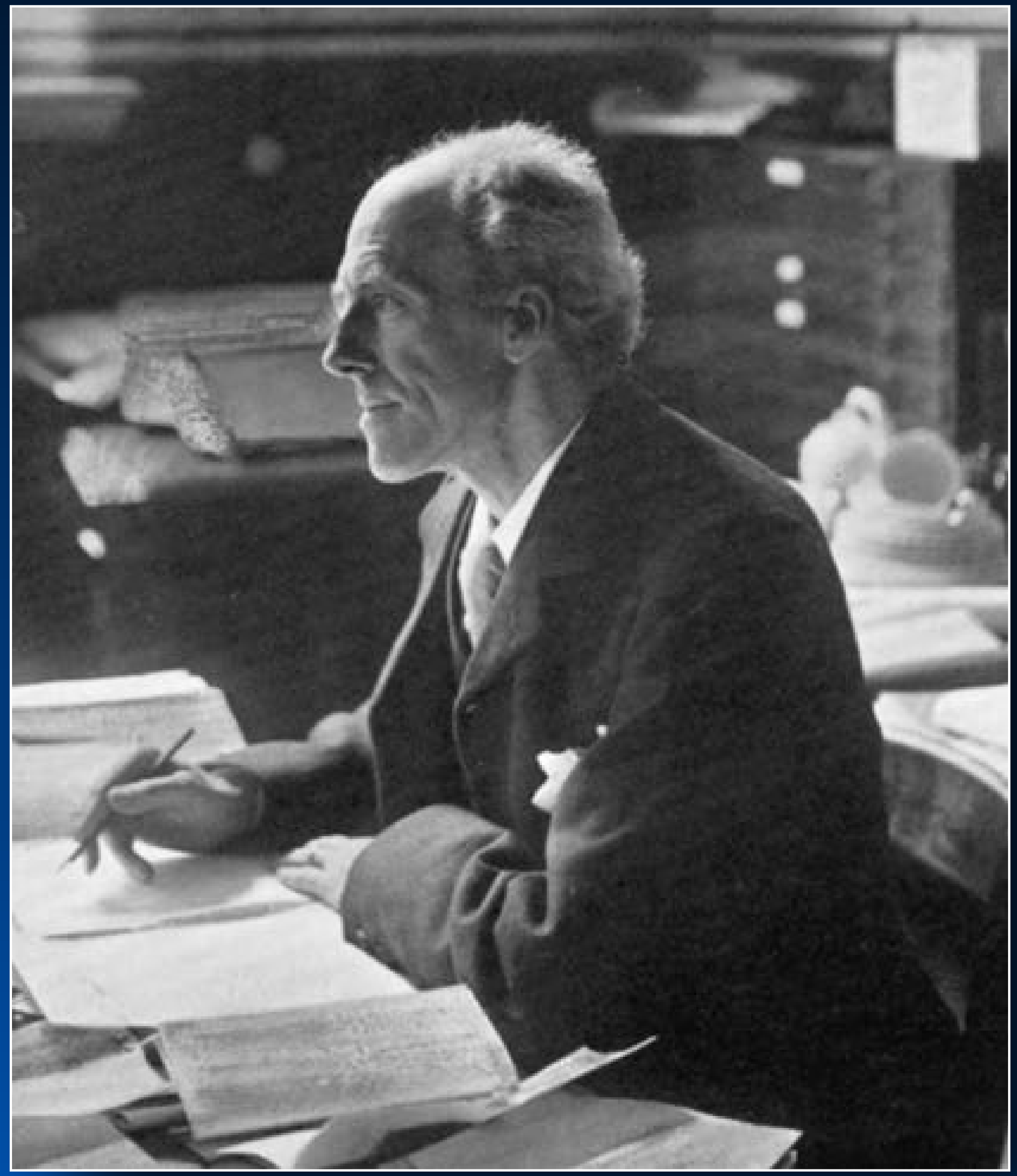
# Tempos & Modes of Macroevolution

## Medelians versus Biometricians



William Bateson
(1861 – 1926)

Though often portrayed as a disagreement between geneticists and morphologists, this debate turned on the question of whether evolution proceeded by natural selection operating on small variations between individuals in a population (Darwin's model) or by discontinuous saltations (Huxley & Galton's model) — on the question of macroevolution.

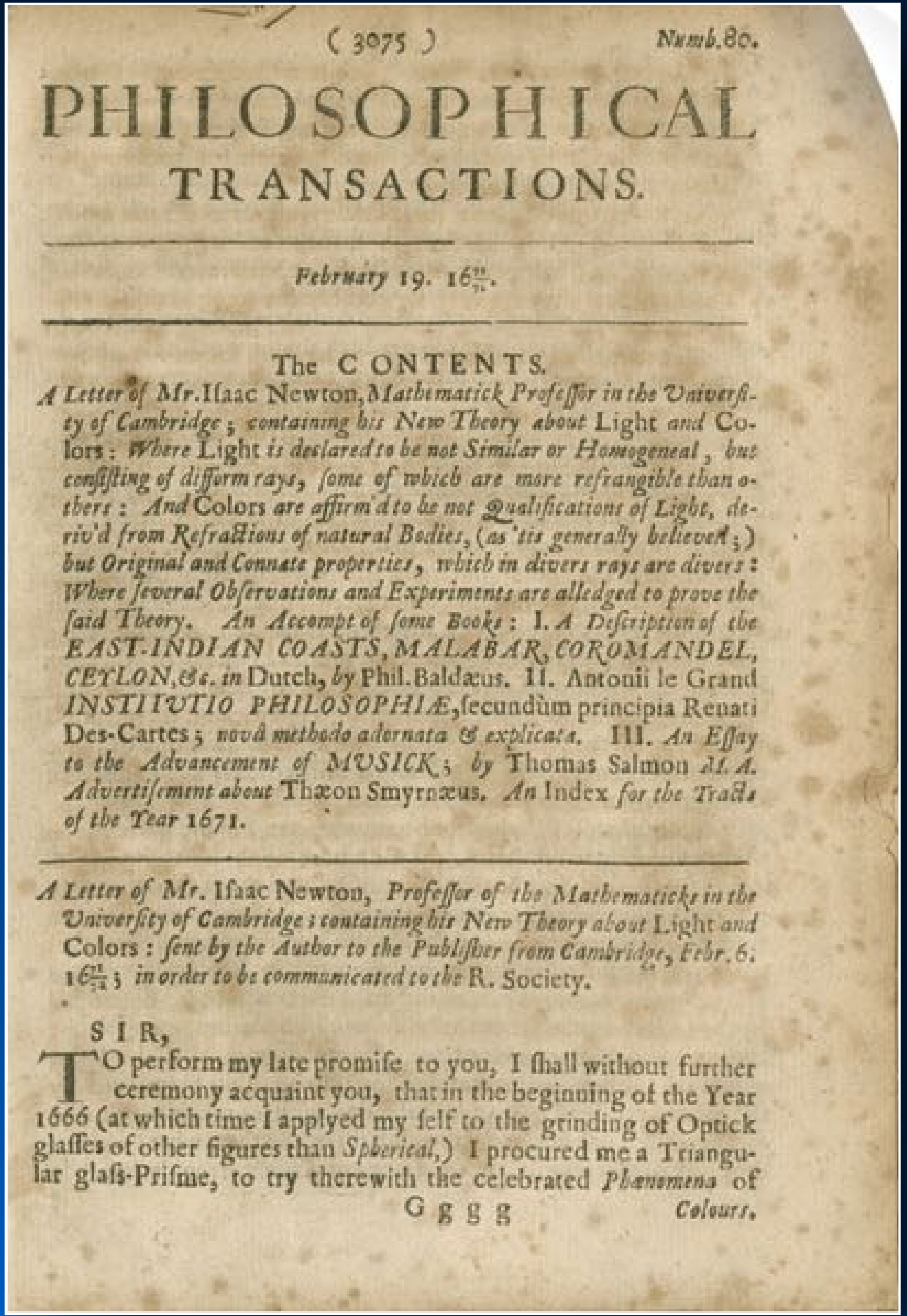


Karl Pearson
(1857 – 1926)

The Mendelians favored Huxley's model and  the biometricians favored Darwin's model. Both had solid theoretical and observational evidence that supported their theories. But logically, neither view of evolution appeared to be compatible with the other.

# Tempos & Modes of Macroevolution

## Founding of *Biometrika*


( 3075 ) Numb. 80.

PHILOSOPHICAL TRANSACTIONS.

*February* 19. 16$\frac{71}{72}$.

The CONTENTS.

*A Letter of* Mr. Isaac Newton, *Mathematick Professor in the University of Cambridge; containing his New Theory about* Light *and* Colors: *Where* Light *is declared to be not Similar or Homogeneal, but consisting of difform rays, some of which are more refrangible than others: And* Colors *are affirm'd to be not Qualifications of Light, deriv'd from Refractions of natural Bodies, (as 'tis generally believed;) but Original and Connate properties, which in divers rays are divers: Where several Observations and Experiments are alledged to prove the said Theory. An Accompt of some Books:* I. *A Description of the EAST-INDIAN COASTS, MALABAR, COROMANDEL, CEYLON, &c. in* Dutch, *by* Phil. Baldæus. II. Antonii le Grand *INSTITUTIO PHILOSOPHIÆ,* secundùm principia Renati Des-Cartes; *novâ methodo adornata & explicata.* III. *An Essay to the Advancement of MUSICK; by* Thomas Salmon *M. A. Advertisement about* Thæon Smyrnæus. *An* Index *for the Tracts of the Year* 1671.

*A Letter of* Mr. Isaac Newton, *Professor of the Mathematicks in the University of Cambridge; containing his New Theory about* Light *and* Colors: *sent by the Author to the Publisher from Cambridge, Febr. 6.* 16$\frac{71}{72}$; *in order to be communicated to the* R. Society.

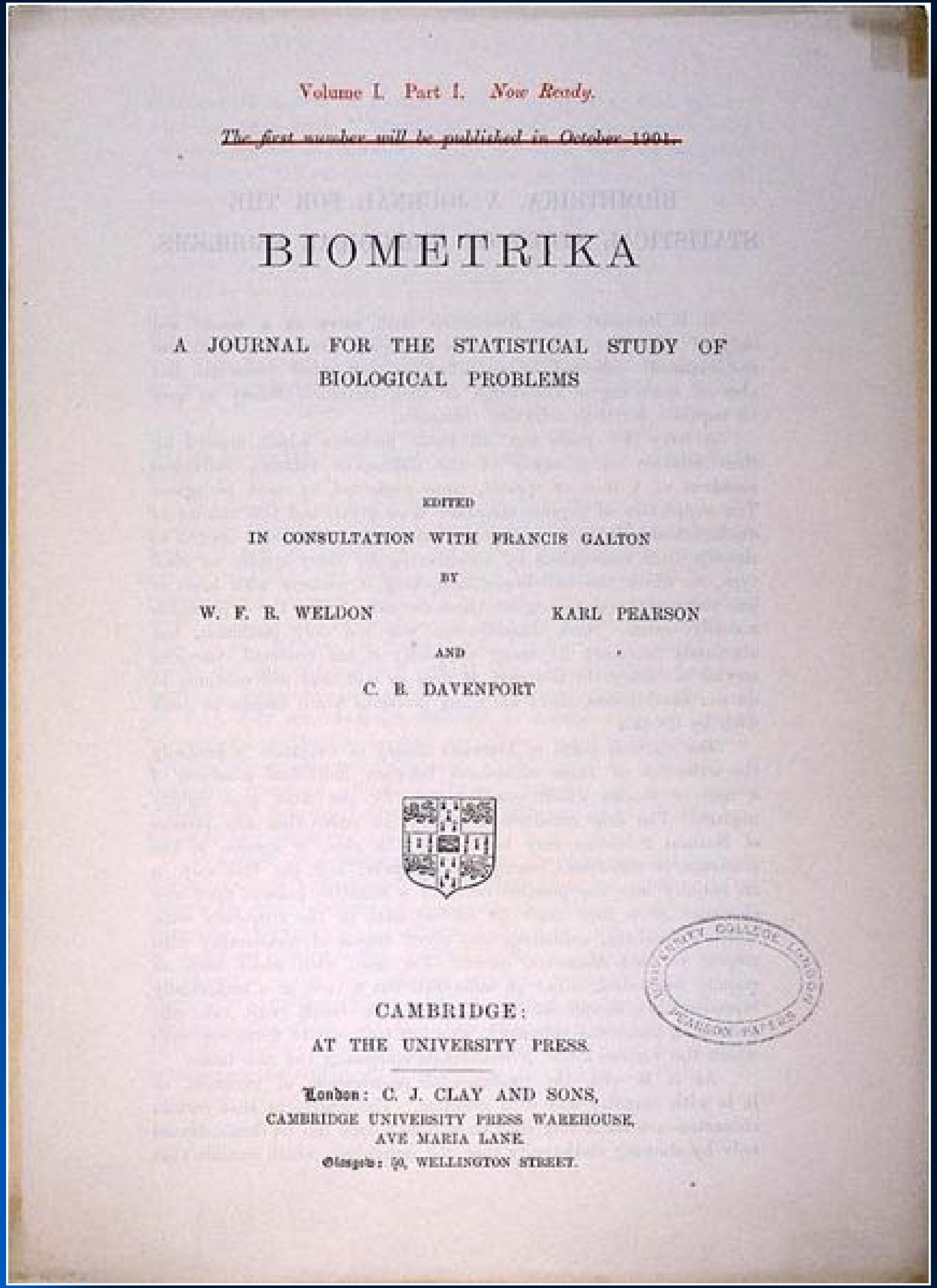
SIR,

TO perform my late promise to you, I shall without further ceremony acquaint you, that in the beginning of the Year 1666 (at which time I applyed my self to the grinding of Optick glasses of other figures than *Spherical*,) I procured me a Triangular glass-Prisme, to try therewith the celebrated *Phænomena* of

Gggg *Colours,*

Bateson criticized Pearson's theory on the grounds that (1) no theoretical distinction existed between differentiation in a single individual and a population and (2) Pearson refused to recognize the distinction between "specific" and "normal" variation.

After unauthorized publication of these criticisms, Pearson, along with his colleague William F. R. Wealdon, broke with the Royal Society (London) and started their own journal, *Biometrika*, to publish research pertaining to the statistical analysis of biological data.


Volume I. Part I. *Now Ready.*

~~*The first number will be published in October 1901.*~~

BIOMETRIKA

A JOURNAL FOR THE STATISTICAL STUDY OF BIOLOGICAL PROBLEMS

EDITED

IN CONSULTATION WITH FRANCIS GALTON

BY

W. F. R. WELDON KARL PEARSON

AND

C. B. DAVENPORT

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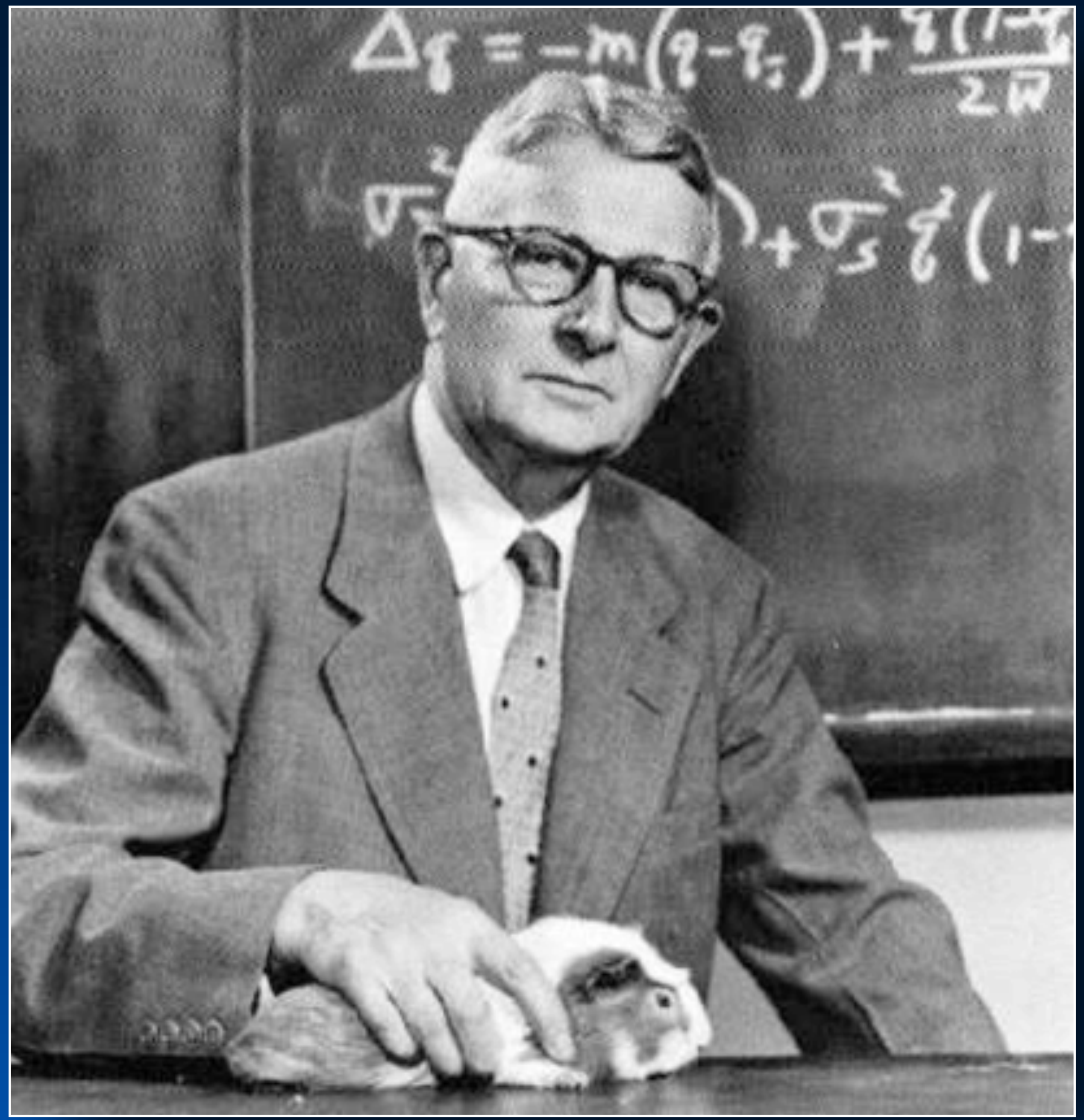
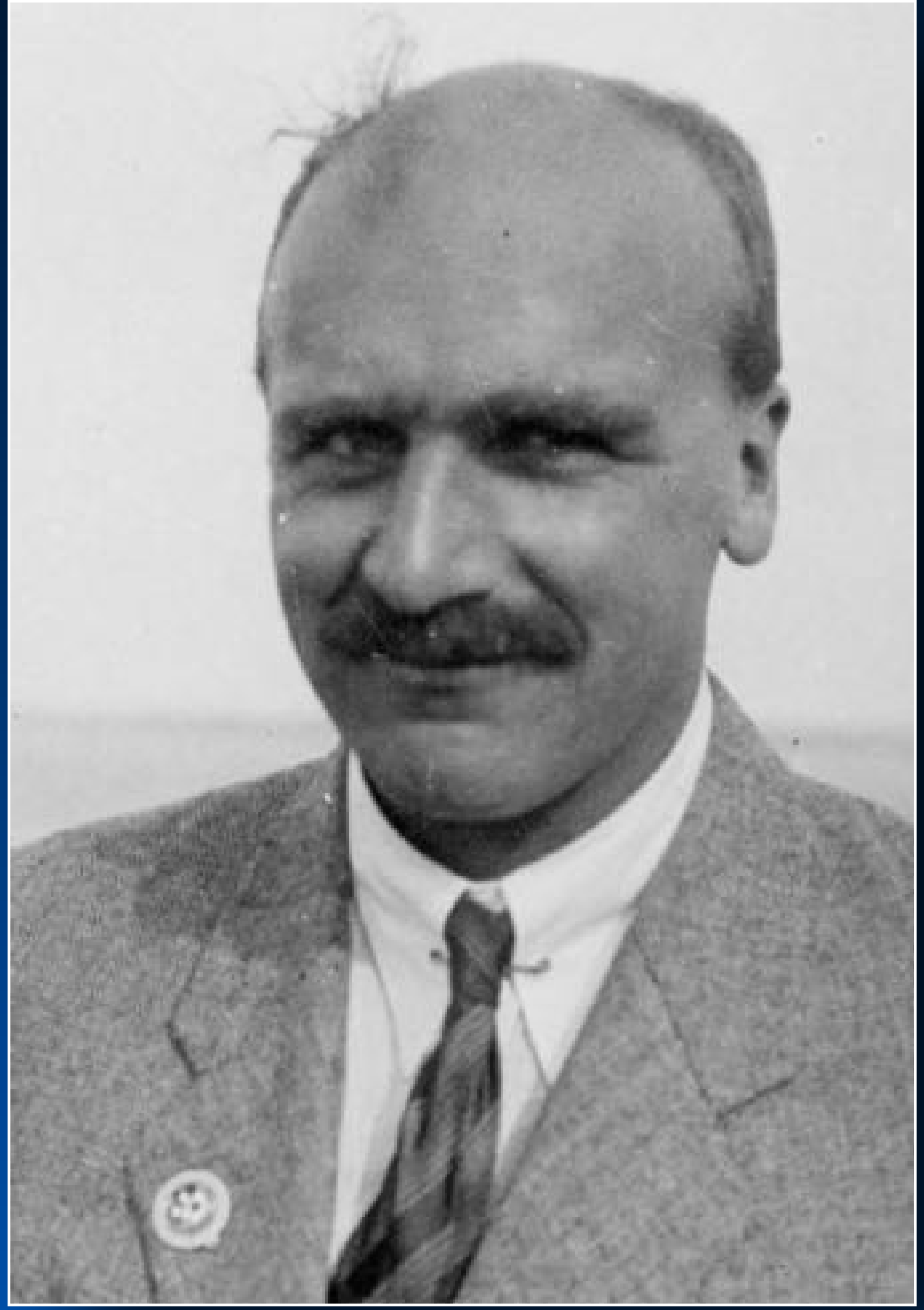
# Tempos & Modes of Macroevolution

## Population Genetics

Ronald Fisher
(1892- 1962)



Sewall Wright
(1889 – 1988)



J. B. S. Haldane
(1882 – 1964)

Resolution of the disagreement between the mendelians and the biometricians over the question of macroevolution was achieved primarily through the efforts of R. A. Fisher, S. Wright and J. B. S. Haldane who, in turn, set the stage for development of the synthetic theory of evolution, also known as the evolutionary synthesis.

# Tempos & Modes of Macroevolution

## Population Genetics

Ronald Fisher
(1892- 1962)

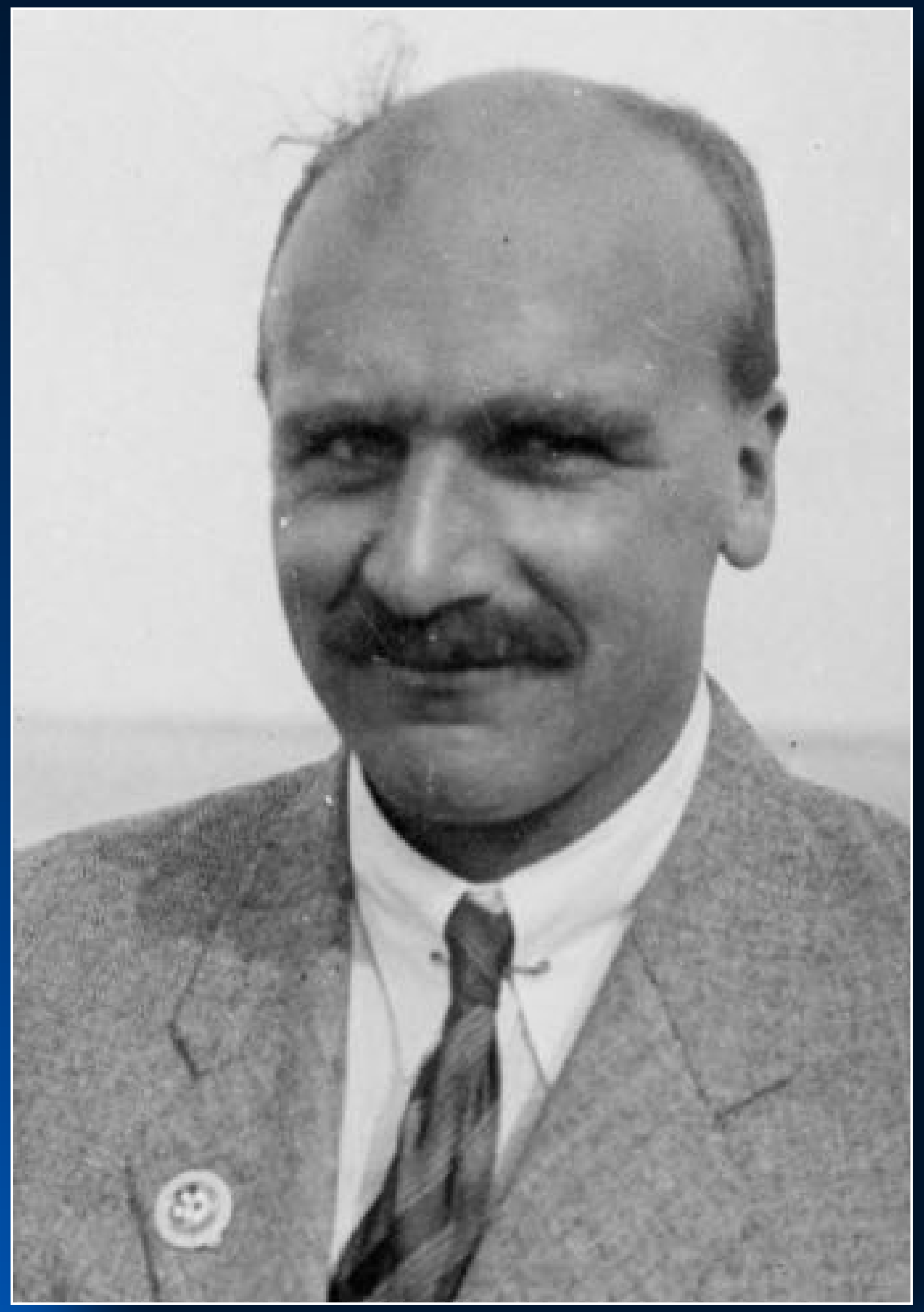
Fisher used mathematical modelling of genetic variance to show that …

- … if a mutant gene (or allele) conferred a survival advantage its frequency would increase in a population;
- … less advantages genes would occur at low frequencies, but could not be eliminated if they were recessive;
- … since most mutations had a small effect on the phenotype, mutation, accompanied by the fixation of advantageous genes, had the effect of changing the range of genetic variation over time.

Thus, over long intervals of time, population phenotypes could achieve substantial changes which would not be lost due to blending or regression to the mean. Fisher's basic insight is now referred to as the Fundamental Theorem of Natural Selection.

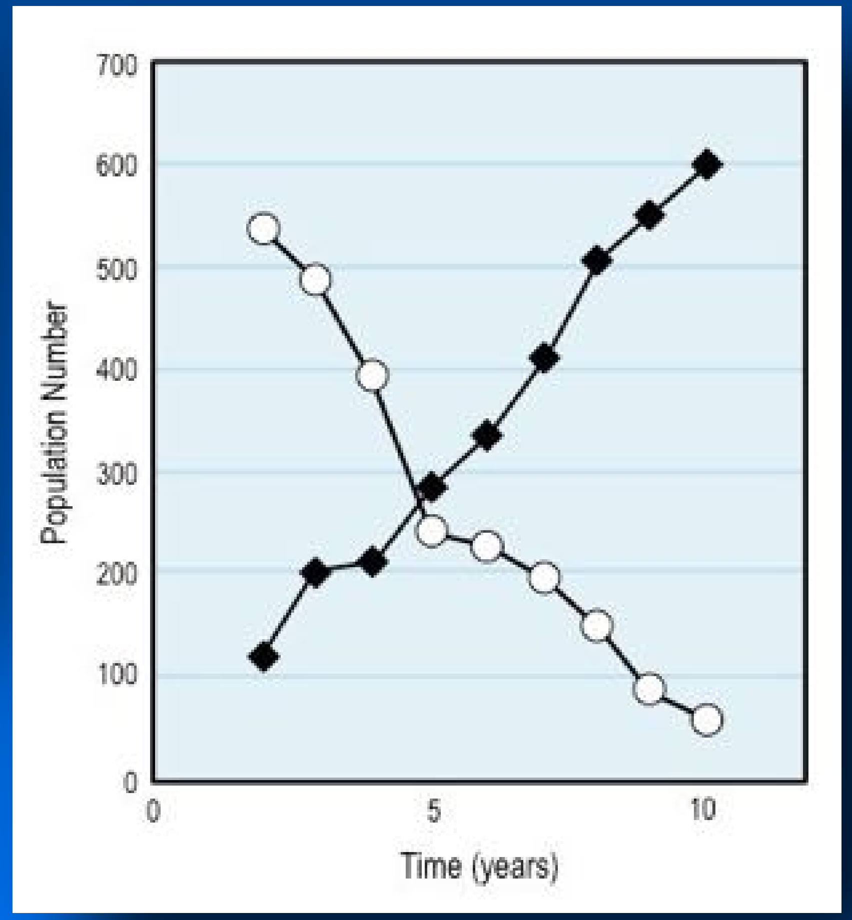
# Tempos & Modes of Macroevolution

## Population Genetics



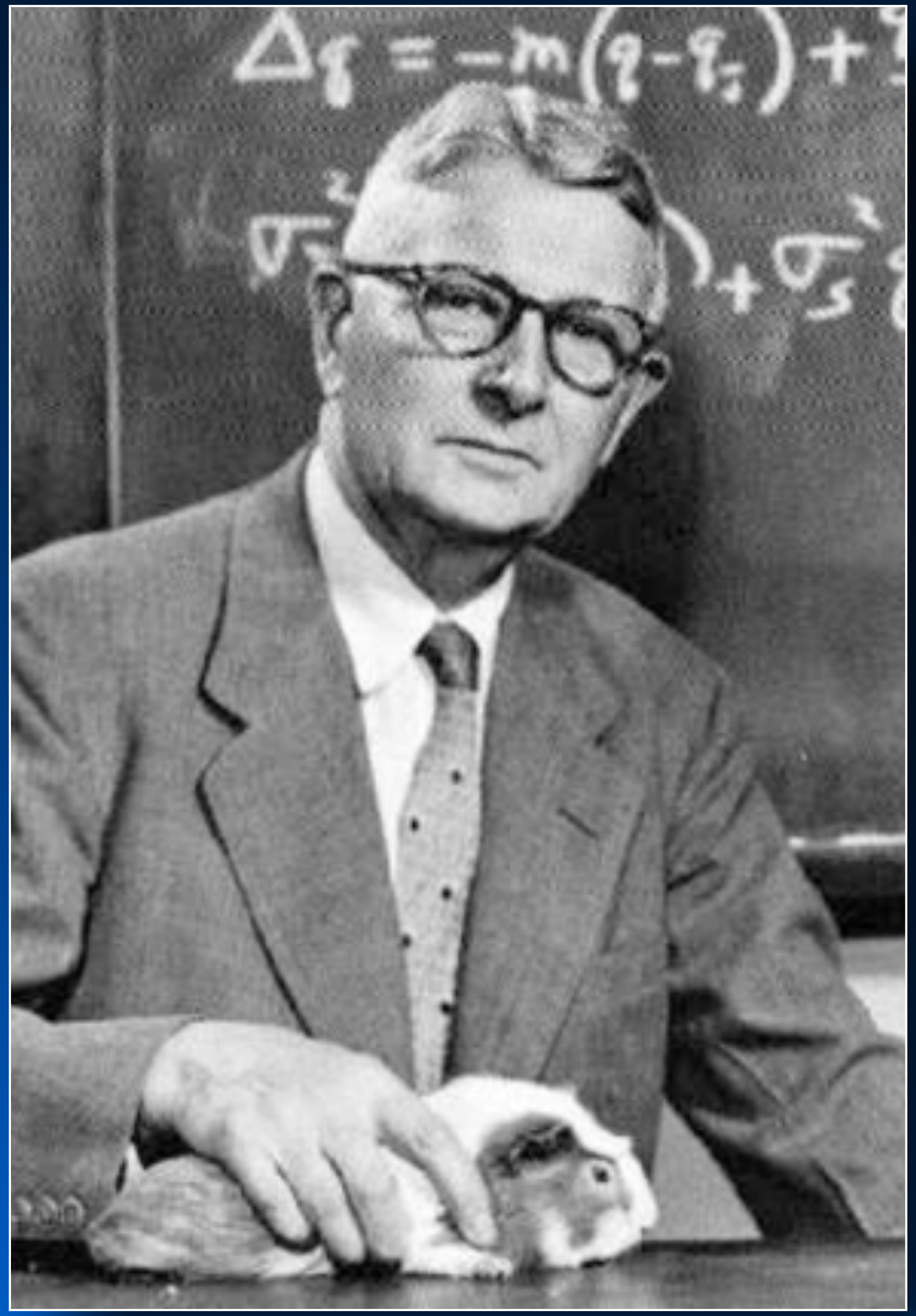
J. B. S. Haldane
(1882 – 1964)

John Haldane was a larger-than-life character who made fundamental contributions to many areas of biology. In evolutionary biology he is best remembered for demonstrating, via observational and mathematical analyses, that natural selection could cause phenotypes to change much more rapidly than Fisher had supposed while still assuming individual mutations would have little effect on the phenotype. His classic experimental verification of this was industrial melanism in the moth *Biston betularia*.




# Tempos & Modes of Macroevolution

## Population Genetics



Sewall Wright
(1889 – 1988)

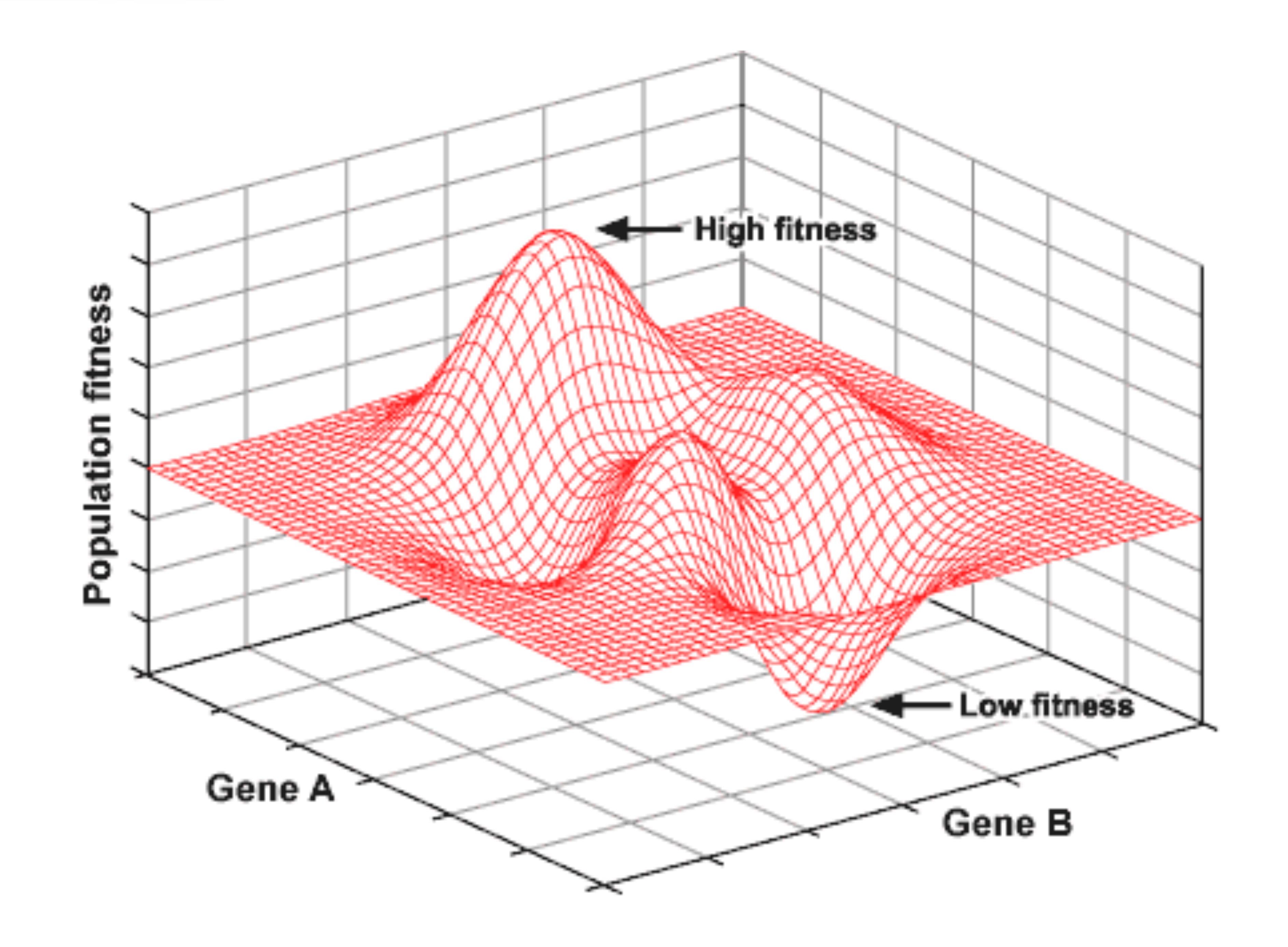
Sewall Wright took Fisher's and Haldane's results and expanded them in new directions by developing a mathematical technique (path analysis) suitable for analyzing interactions between gene systems. He showed that novel genotypes could be fixed over short intervals of time via interbreeding in small, isolated populations. Once established, these new genotypes (and the phenotypes that resulted) could be operated on by natural selection as the small population expanded its range.

From an optimization point-of-view Wright suggested that natural selection would be most effective in geographically widespread species that had been broken up into isolated or semi-isolated populations in which interbreeding was common . Wright also developed a powerful visual metaphor for evolution, the "adaptive landscape".

# Tempos & Modes of Macroevolution

## Population Genetics

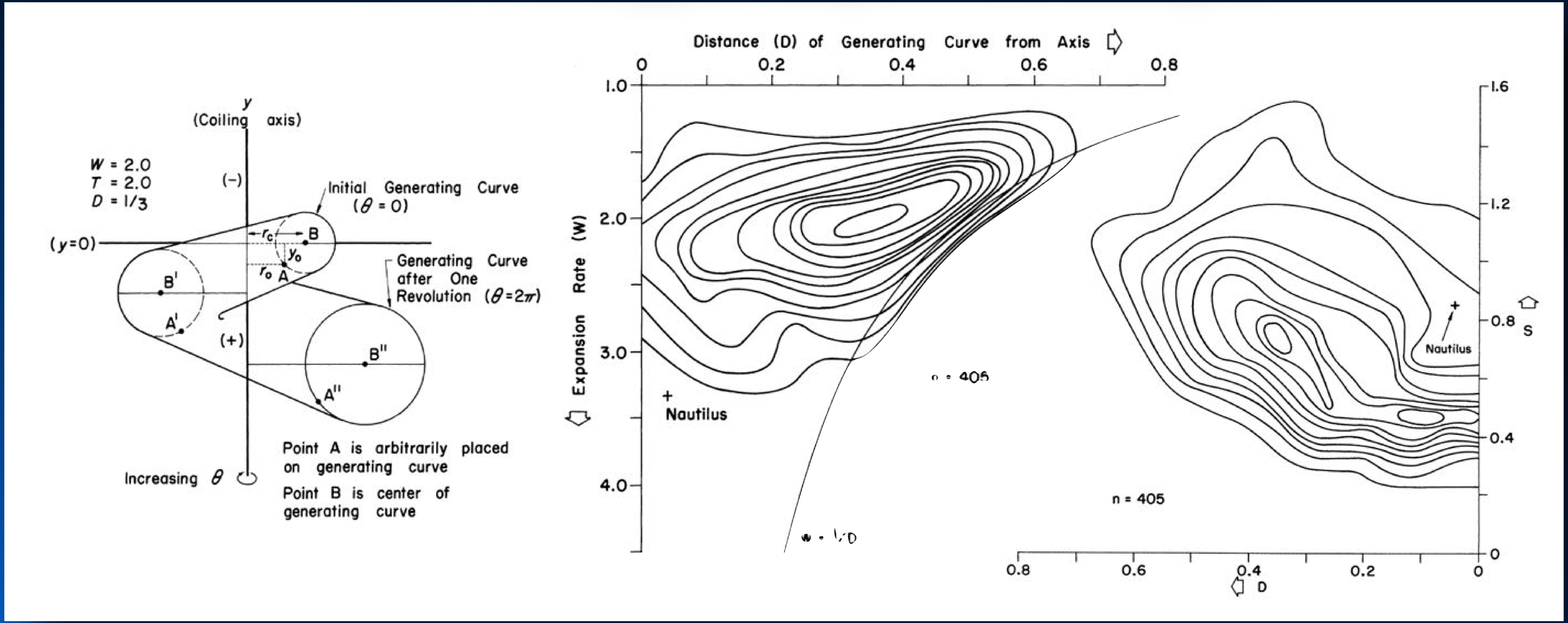
The Adaptive “Fitness” Landscape




- Expresses the evolutionary fitness of different combinations of alleles as a surface composed of both local and global minima/maxima.
- Evolution operates to drive populations up their local fitness slopes via directional changes in the range of genetic variance over time.
- Different local maxima can be regarded as equivalent to taxonomic species and ecological niches.
- Over time the landscape is dynamic since different environmental conditions will favor different gene/allel combinations.
- The landscape model works as well for phenotypes (= forms) as it does for genotypes thus allowing it to be applied to fossil, as well as Recent, species.

# Tempos & Modes of Macroevolution

## The Phenotypic Adaptive Landscapes

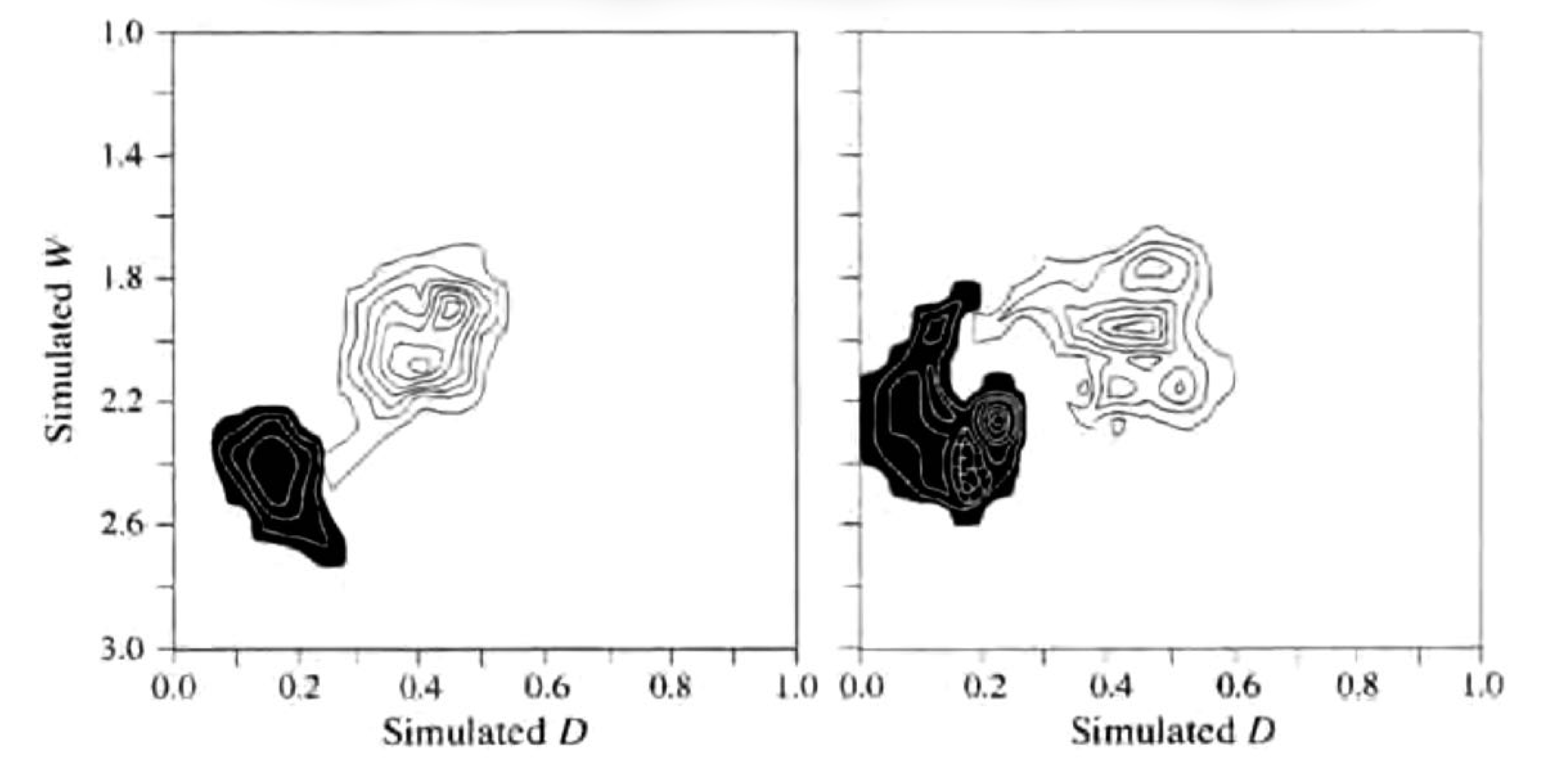



In a series of theoretical paleobiological studies Raup employed Wright's adaptive landscape metaphor as a means of quantifying the shape spaces of coiled molluscs. These diagrams show the shape space of 405 planispirally coiled ammonites according to Raup's coiling parameters $W$, $D$ and $S$.

Diagrams from Raup (1966, 1967)

# Tempos & Modes of Macroevolution

## The Phenotypic Adaptive Landscapes




Later, as a project for Raup's Quantitative Methods in Paleobiology class, I used the same adaptive landscape metaphor to show that the coiling distinction between fossil nautiloids and fossil ammonites could not be attributed to morphological displacement between the two clades.

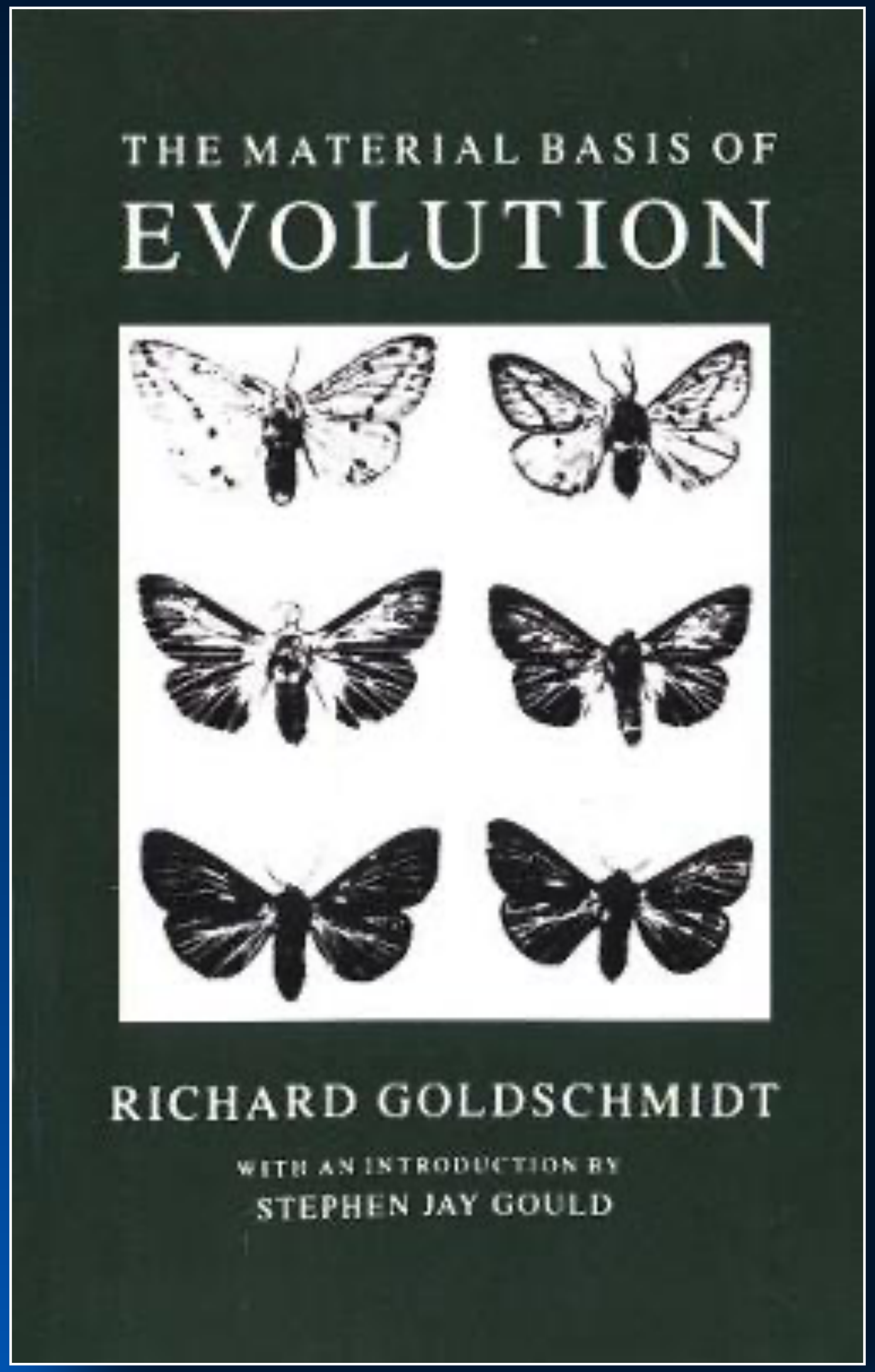
Diagrams from MacLeod (2002)

# Tempos & Modes of Macroevolution

## Richard Goldschmidt & Hopeful Monsters

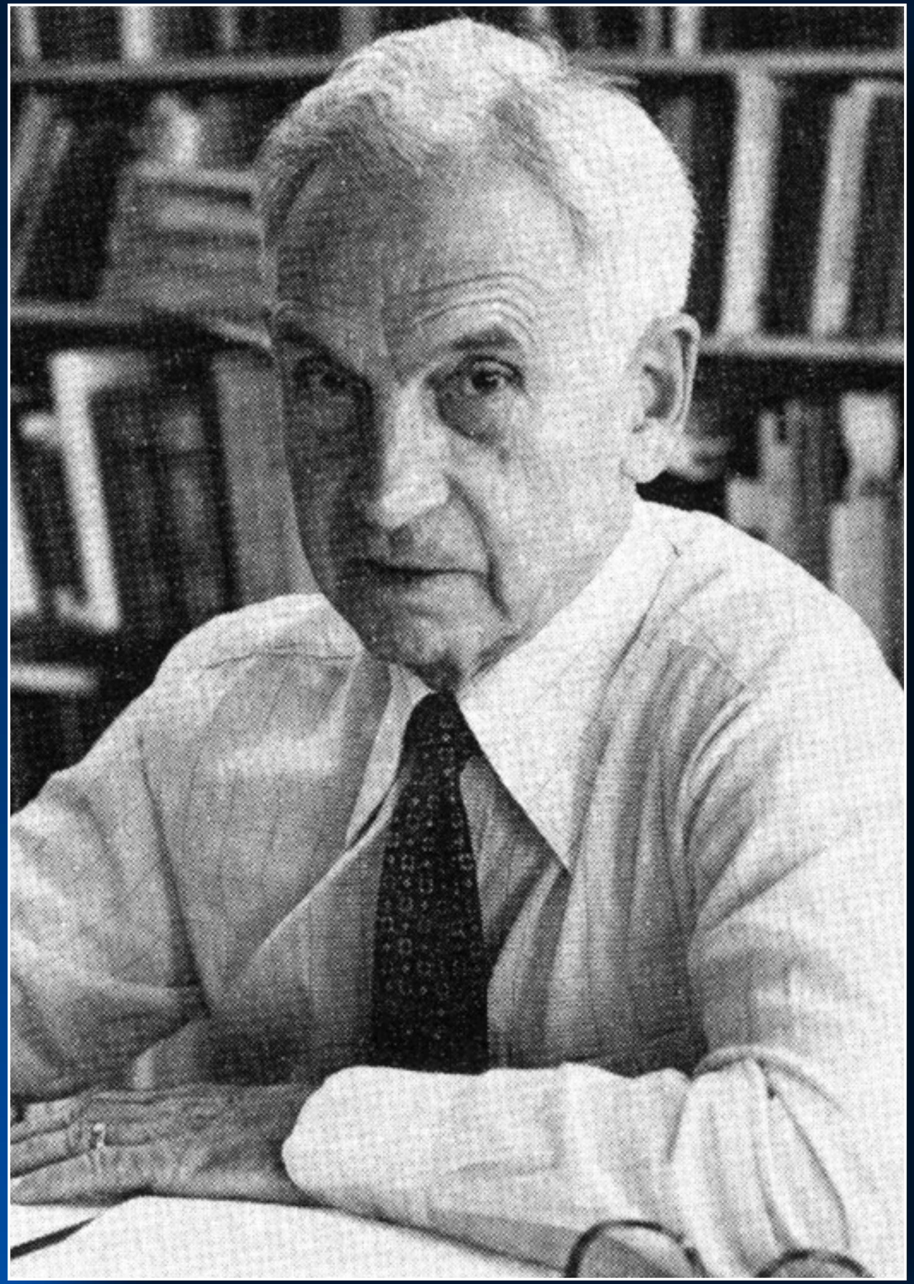
Richard Goldschmidt
(1878- 1958)

A German-American geneticist Richard Goldschmidt was one of the first biologists to attempt to integrate genetics, development and evolution. While Goldschmidt accepted the findings of the population geneticists, he remained skeptical that mutations resulting in small phenotypic changes were the only ones that occurred or that these could be responsible for major phenotypic transitions. Instead, he proposed the existence of macromuations: mutations that effected whole organ systems of developmental pathways. Goldschmidt used the term “hopeful monster” to refer to the product of a macromutation and the potential ancestor of a new evolutionary lineage. However, this idea was criticized on the basis of the well-known cost of rarity.

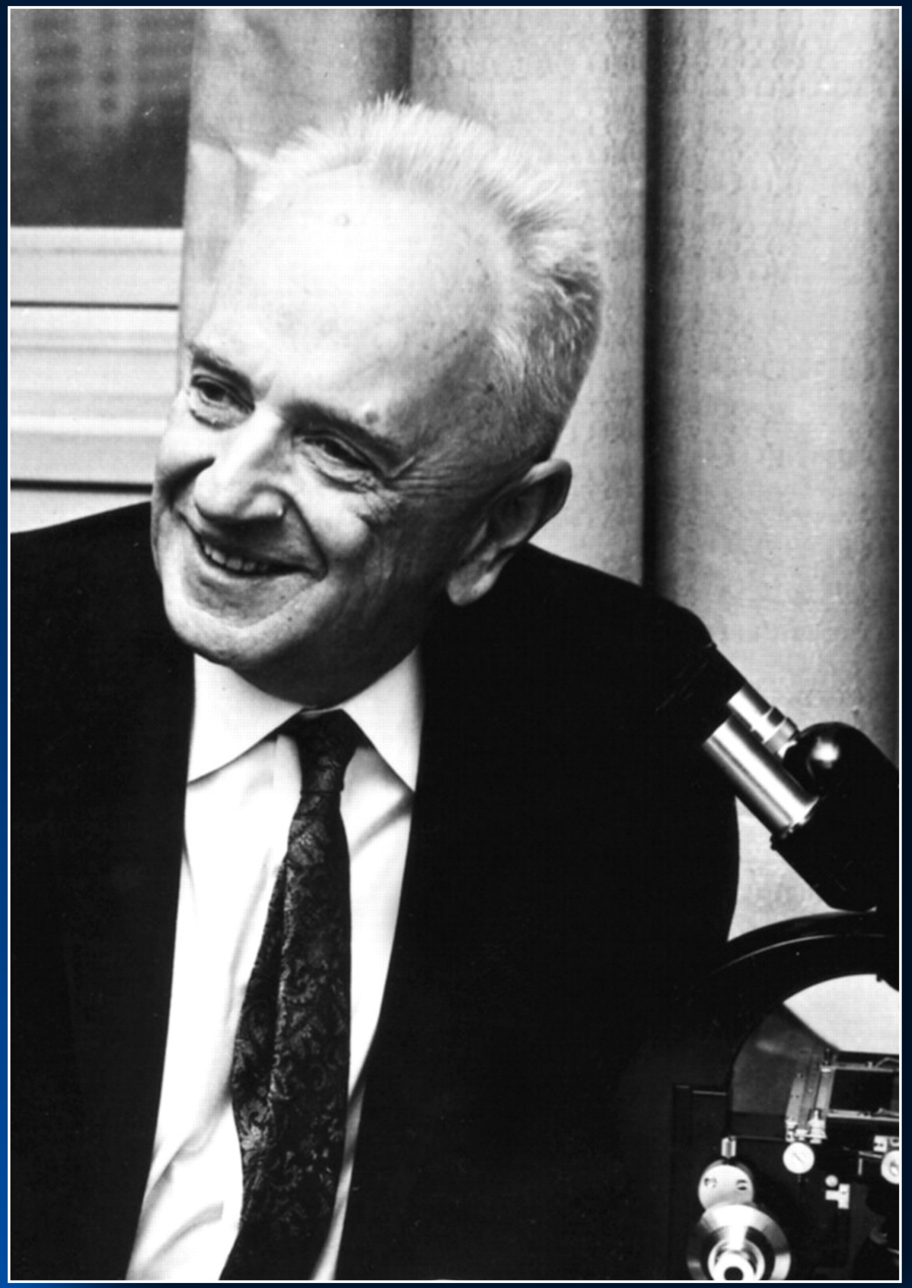


# Tempos & Modes of Macroevolution

## The Neo-Darwinian Evolutionary Synthesis



Ernst Mayr
(1904 - 2005)



Theodosius Dobzhansky
(1900 - 1975)

George G. Simpson
(1902 – 1984)

Drawing on the mechanistic and mathematical advances that had been achieved by the population geneticists, biologists, and taxonomists, paleontologists began abandoning their commitment to macroevolution as a distinct set of processes responsible the high-level structure of species and phenotypic trends seen in the fossil record.

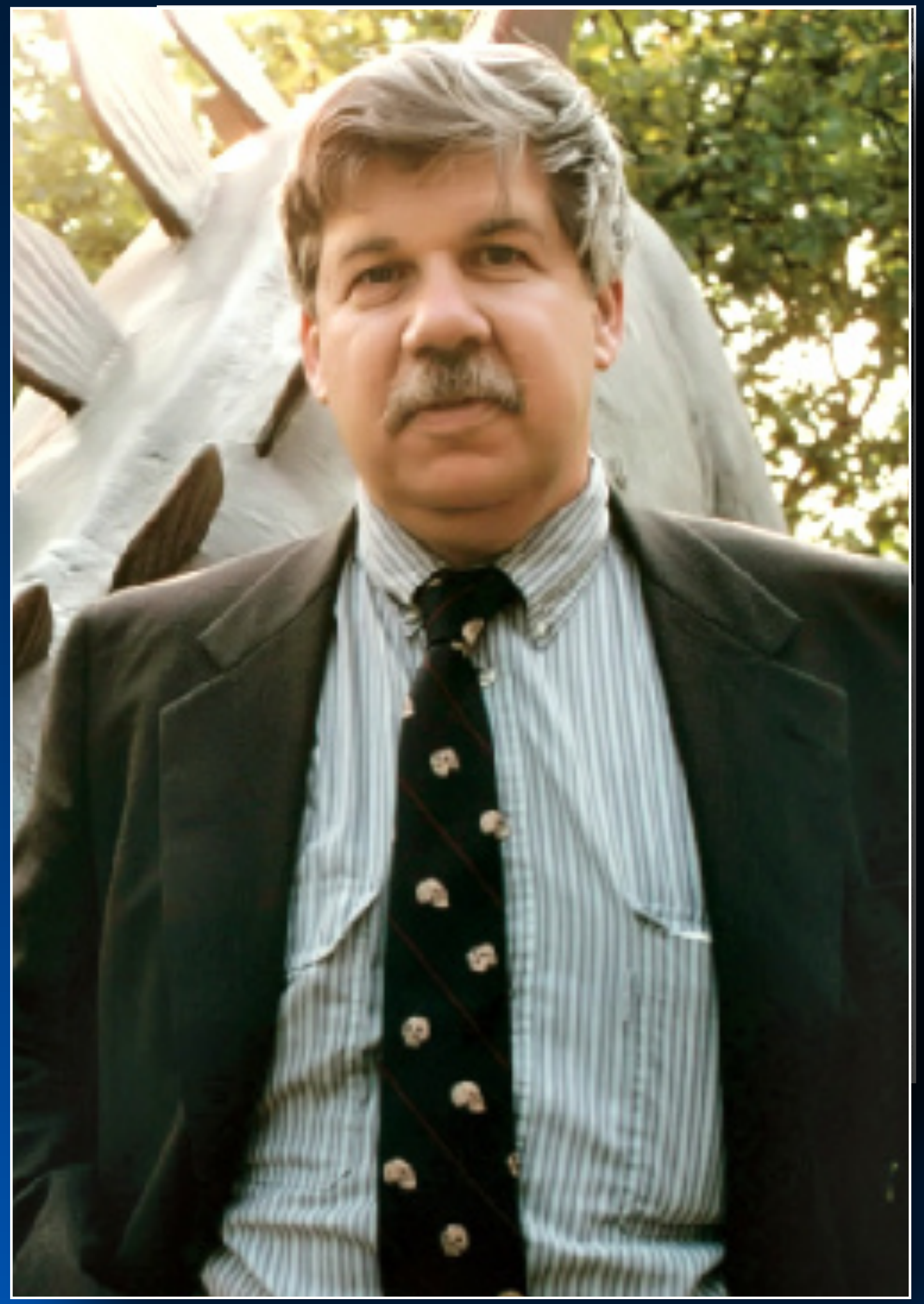
# Tempos & Modes of Macroevolution

## The Neo-Darwinian Evolutionary Synthesis

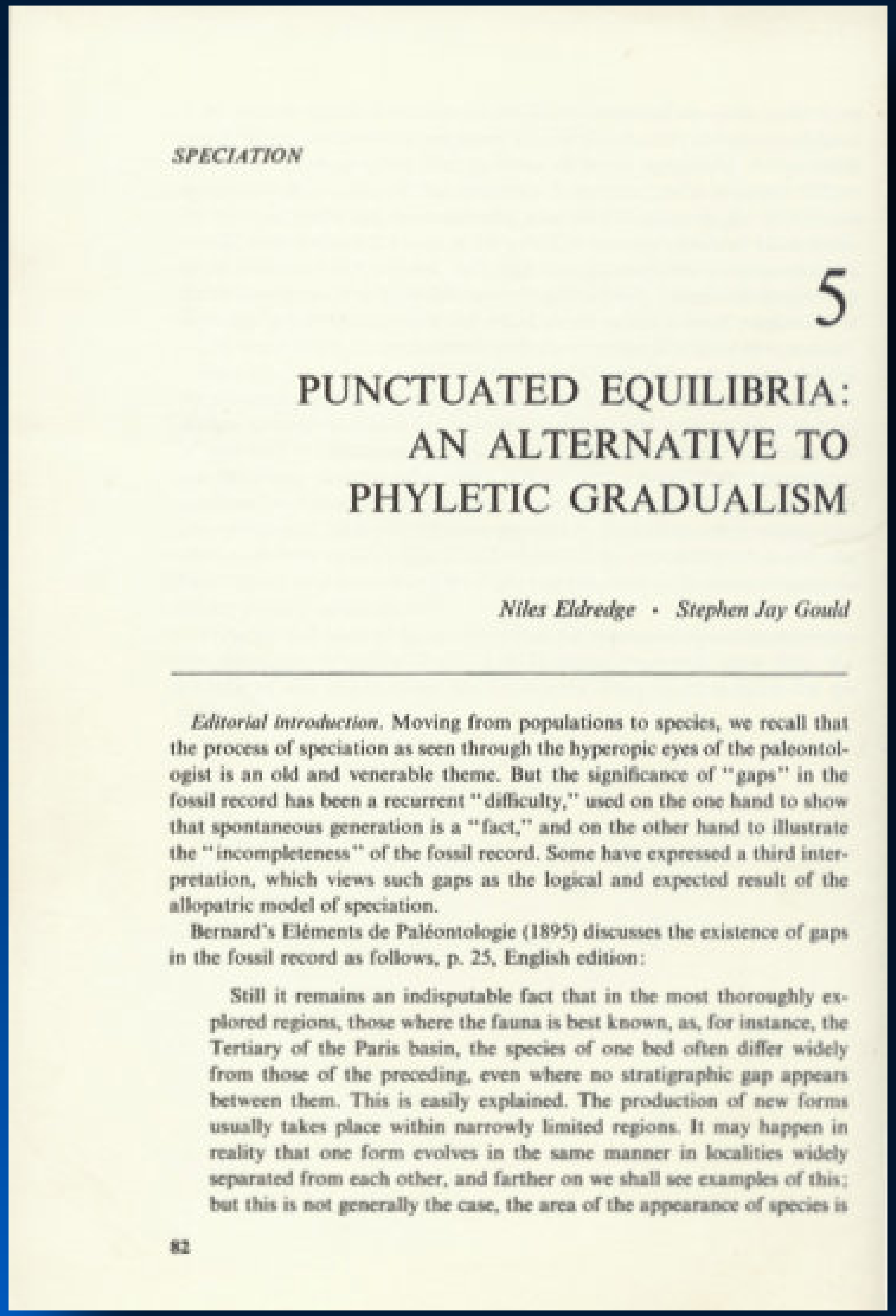
- All evolutionary phenomena can be explained by known genetic mechanisms.
- Evolutionary change is gradual and caused by natural selection operating on small phenotypic changes that, in turn, are manifestations of generic changes.
- Natural selection is the driver of evolutionary change and operates even if the fitness differences between individuals in a population is slight.
- Selection operates directly on the phenotype, but since the heritable aspects of phenotype are determined by the genotype, evolution comes about via the fixation of changes in the genotype with the gene representing the ultimate unit of selection.
- Apparent discontinuities between species, observed in the Recent and in the fossil record, originate via gradual phenotypic divergence from ancestors (promoted by the genetic isolation of small populations), but are rarely preserved in the fossil record due to its incomplete nature.
- Apparent long-term trends that exist in the fossil record can be explained by the mechanisms listed above.

# Tempos & Modes of Macroevolution

## Punctuated Equilibria: A Challenge to Neo-Darwinian Evolutionary Synthesis



Stephen J. Gould
(1941 - 2002)



SPECIATION

5

PUNCTUATED EQUILIBRIA:
AN ALTERNATIVE TO
PHYLETIC GRADUALISM

*Niles Eldredge • Stephen Jay Gould*

*Editorial introduction.* Moving from populations to species, we recall that the process of speciation as seen through the hyperopic eyes of the paleontologist is an old and venerable theme. But the significance of "gaps" in the fossil record has been a recurrent "difficulty," used on the one hand to show that spontaneous generation is a "fact," and on the other hand to illustrate the "incompleteness" of the fossil record. Some have expressed a third interpretation, which views such gaps as the logical and expected result of the allopatric model of speciation.

Bernard's Eléments de Paléontologie (1895) discusses the existence of gaps in the fossil record as follows, p. 25, English edition:

> Still it remains an indisputable fact that in the most thoroughly explored regions, those where the fauna is best known, as, for instance, the Tertiary of the Paris basin, the species of one bed often differ widely from those of the preceding, even where no stratigraphic gap appears between them. This is easily explained. The production of new forms usually takes place within narrowly limited regions. It may happen in reality that one form evolves in the same manner in localities widely separated from each other, and farther on we shall see examples of this; but this is not generally the case, the area of the appearance of species is

82

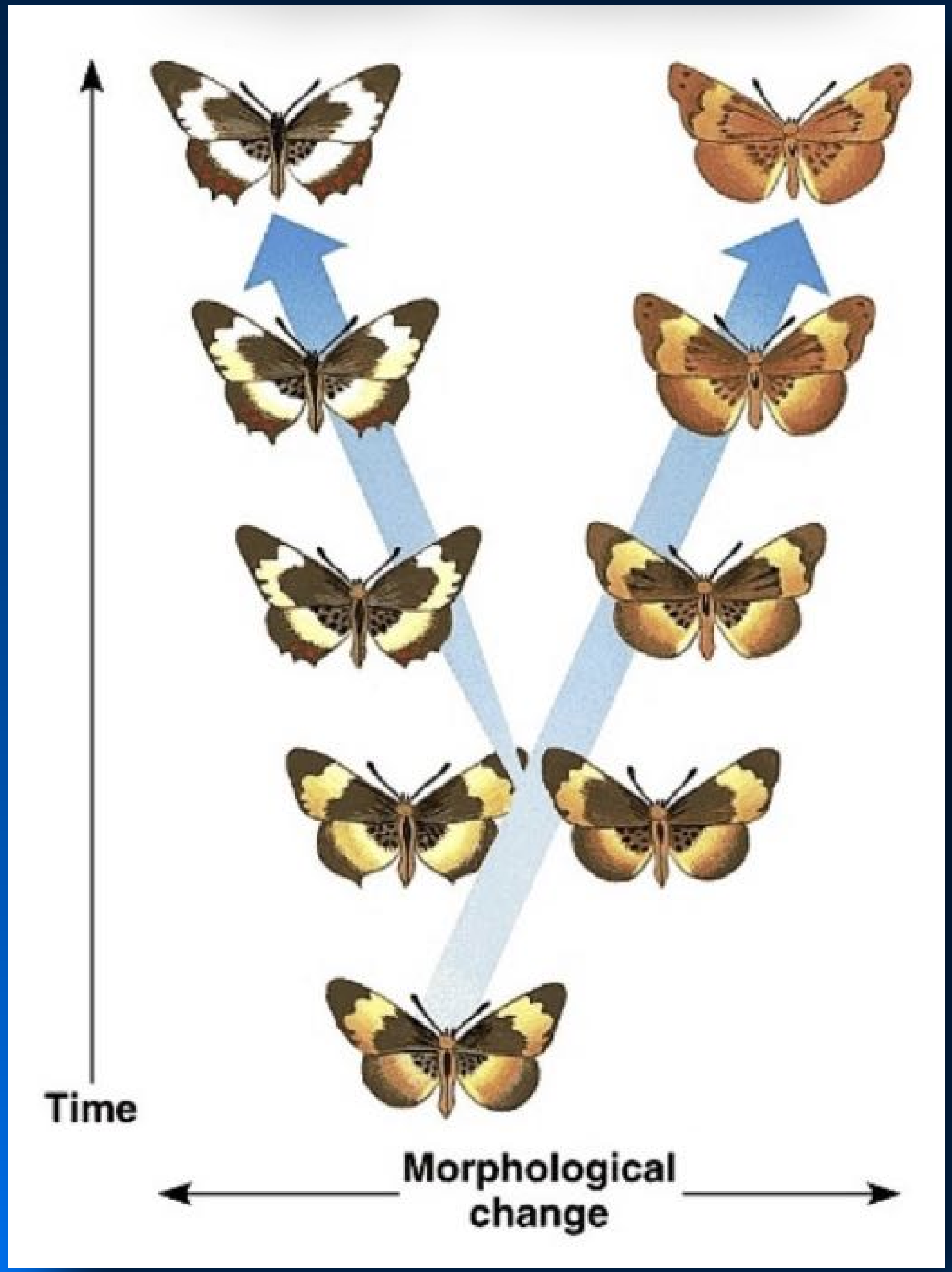
Niles Eldredge
(b. 1943)

Eldredge, N., and Gould, S.J., 1972, Punctuated equilibria: An alternative to phyletic gradualism, in Schopf, T.J.M. ed., Models in Paleobiology, San Francisco, Freeman Cooper & Company, p. 82–115.

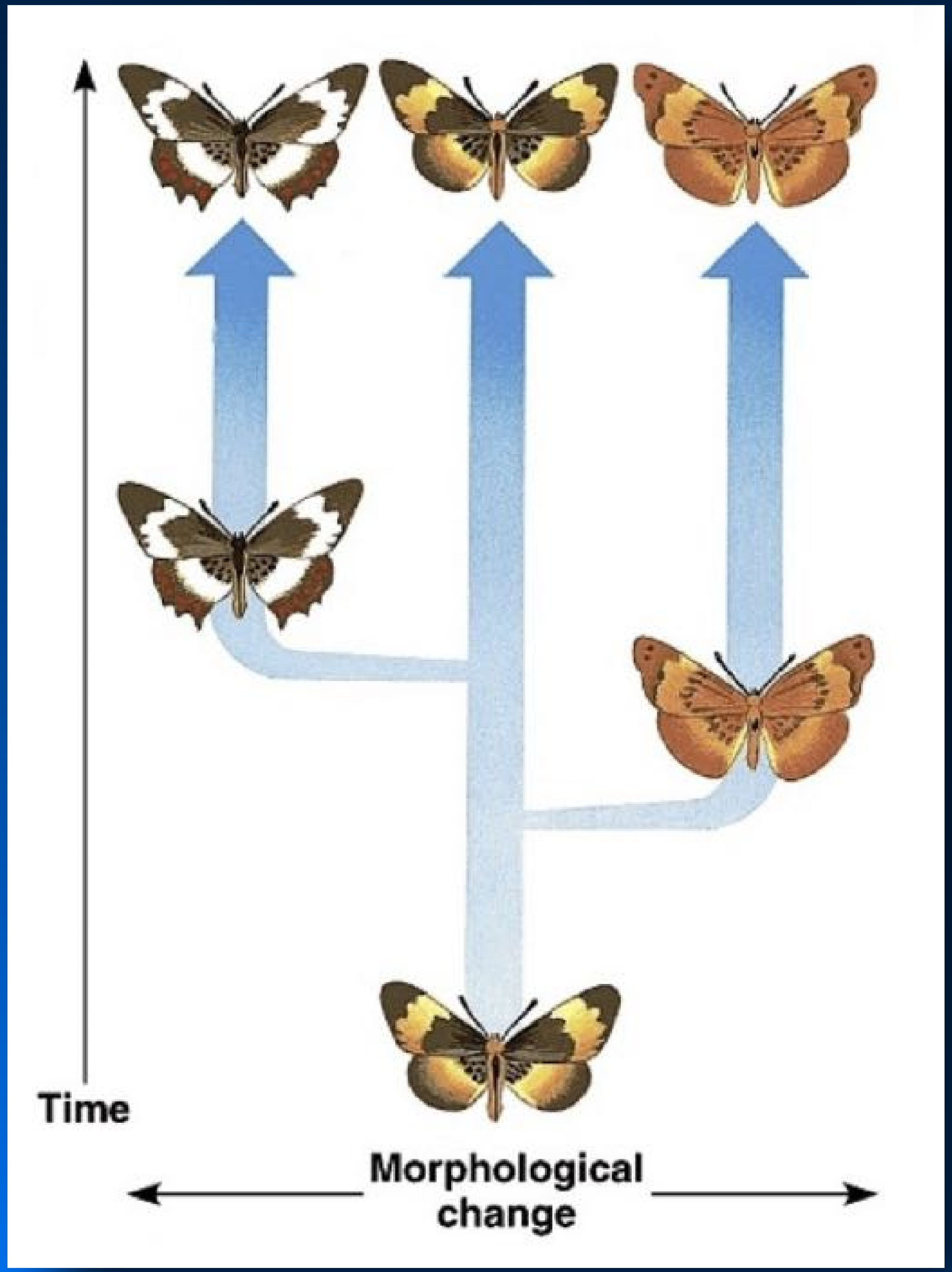
# Tempos & Modes of Macroevolution

## Punctuated Equilibria: A Challenge to Neo-Darwinian Evolutionary Synthesis

### Phyletic Gradualism




### Punctuated Equilibria

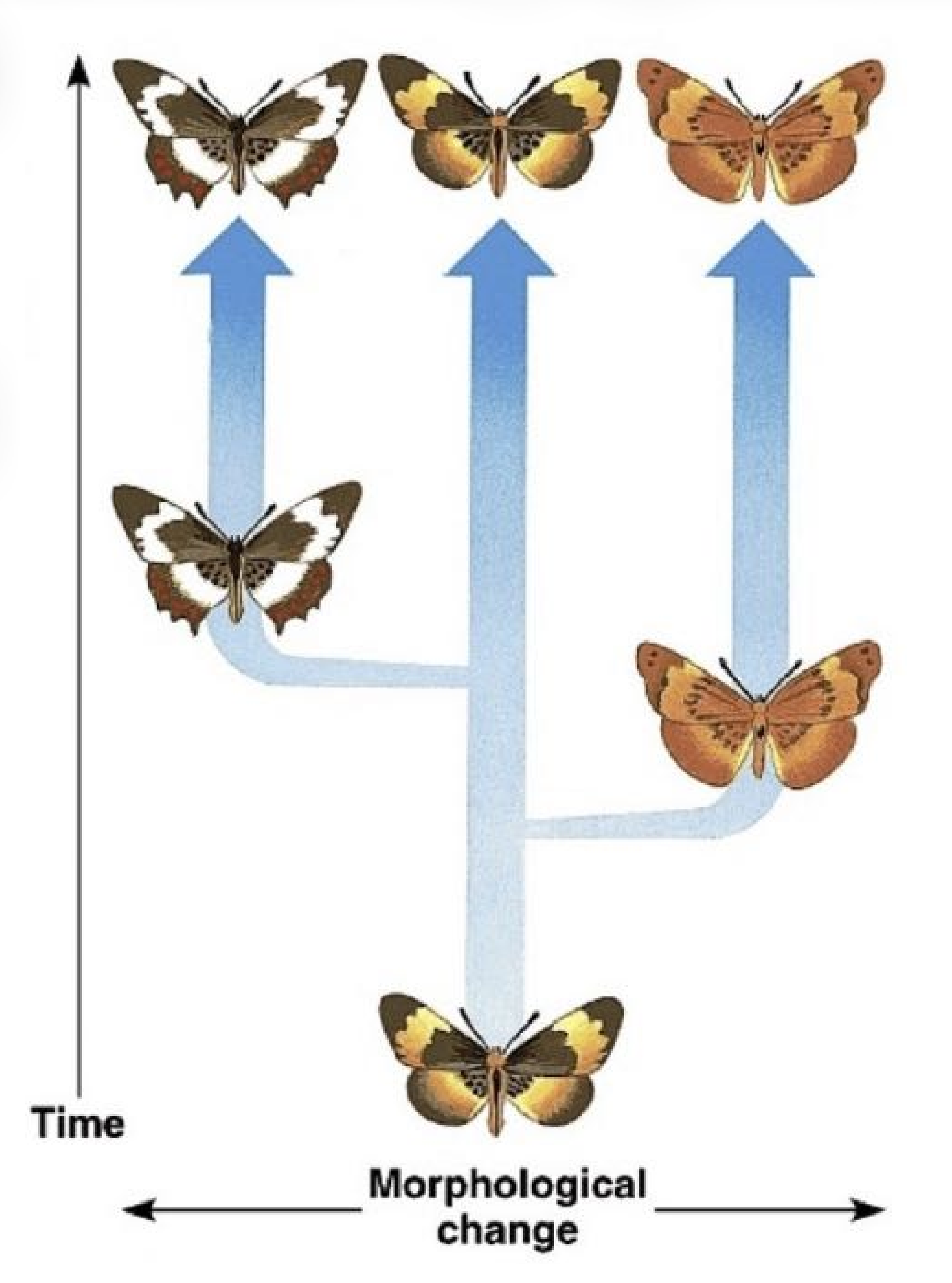


# Tempos & Modes of Macroevolution

## Punctuated Equilibria: A Challenge to Neo-Darwinian Evolutionary Synthesis

Paleontologists had focused on the lack of intermediate forms as evidence for saltation as the dominant mode of macroevolution. Population geneticists countered that, species could be formed from small isolated populations on the periphery of an ancestral species' distribution. Since these intermediate populations would have little chance of ever entering the fossil record the record of gradual change would be lost.

- Paleontologists lost the argument for macroevolution when they could not propose a mechanism whereby it could arise that was consistent with genetic data.
- Gould and Eldredge found a way around the geneticists' rebuttal by arguing that once formed, most species did not undergo morphological change in response to environmental changes as the neo-Darwnian model predicted they should. Morphological/phenotypic change was concentrated in the speciation event itself. Hence their mantra: "Stasis is data".



# Tempos & Modes of Macroevolution

## Evidence For Punctuated Equilibria

*Phacops rana*

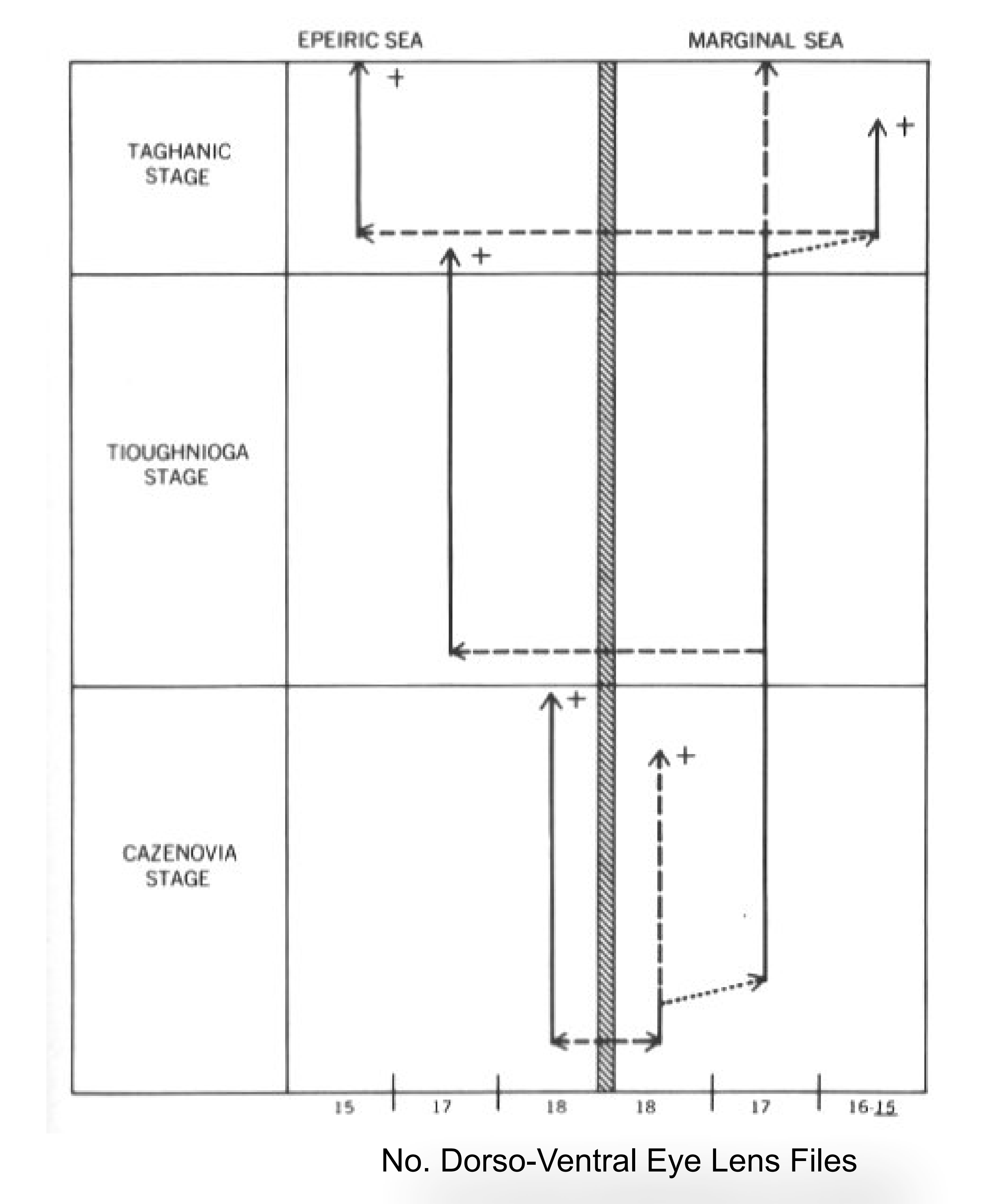
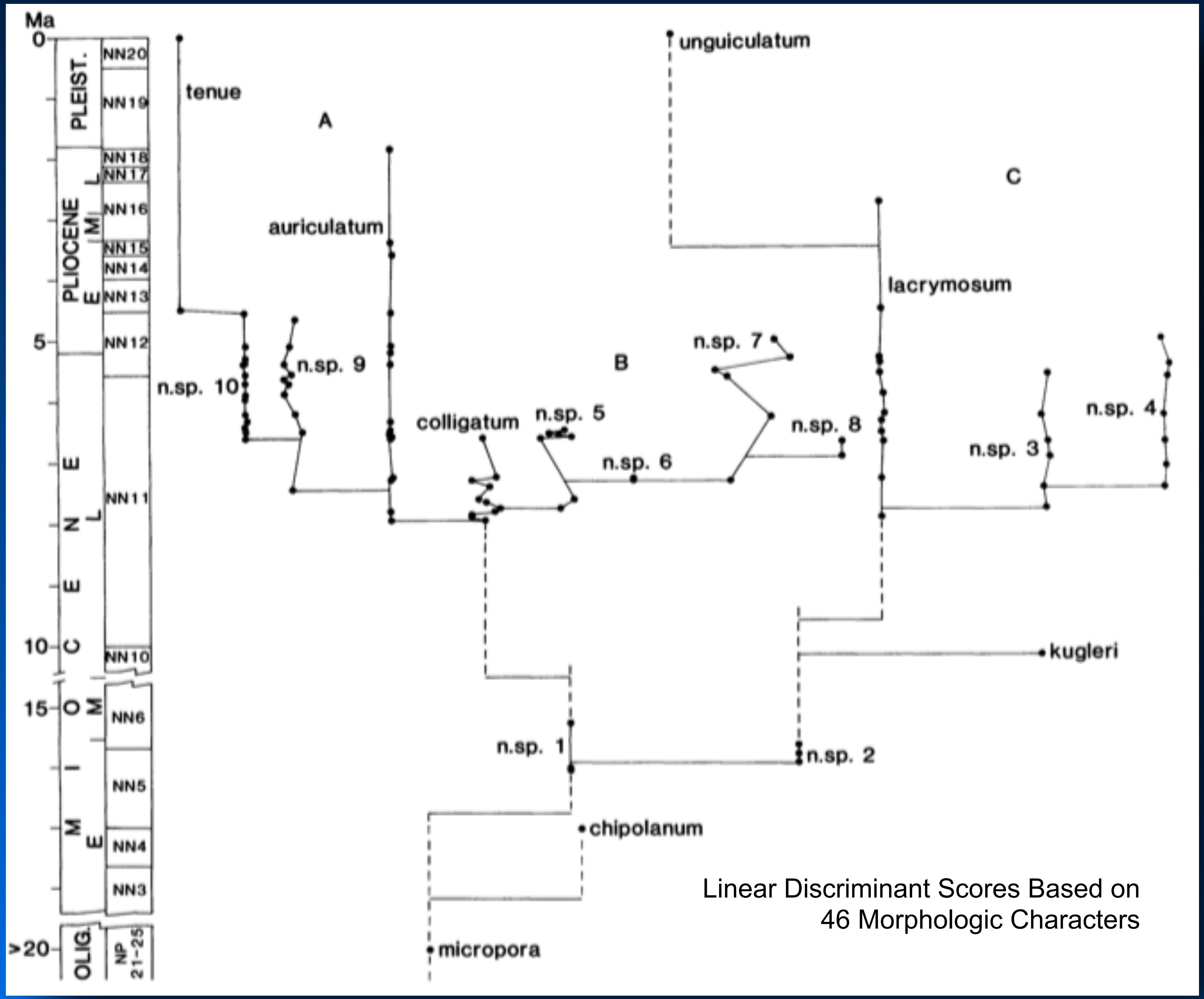


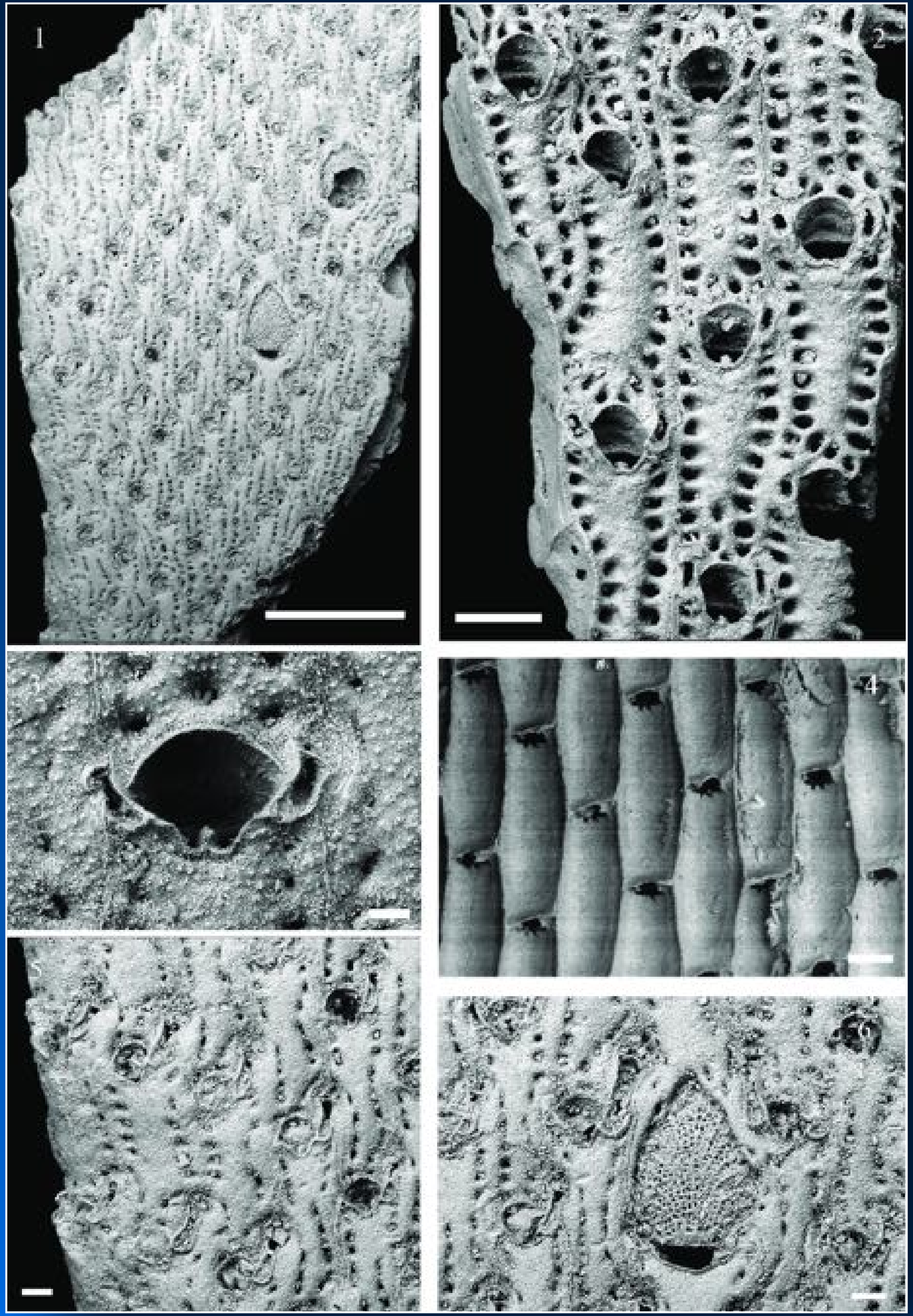

Diagram from Eldredge and Gould (1972)

# Tempos & Modes of Macroevolution

## Evidence For Punctuated Equilibria

*Metrarabdotos*



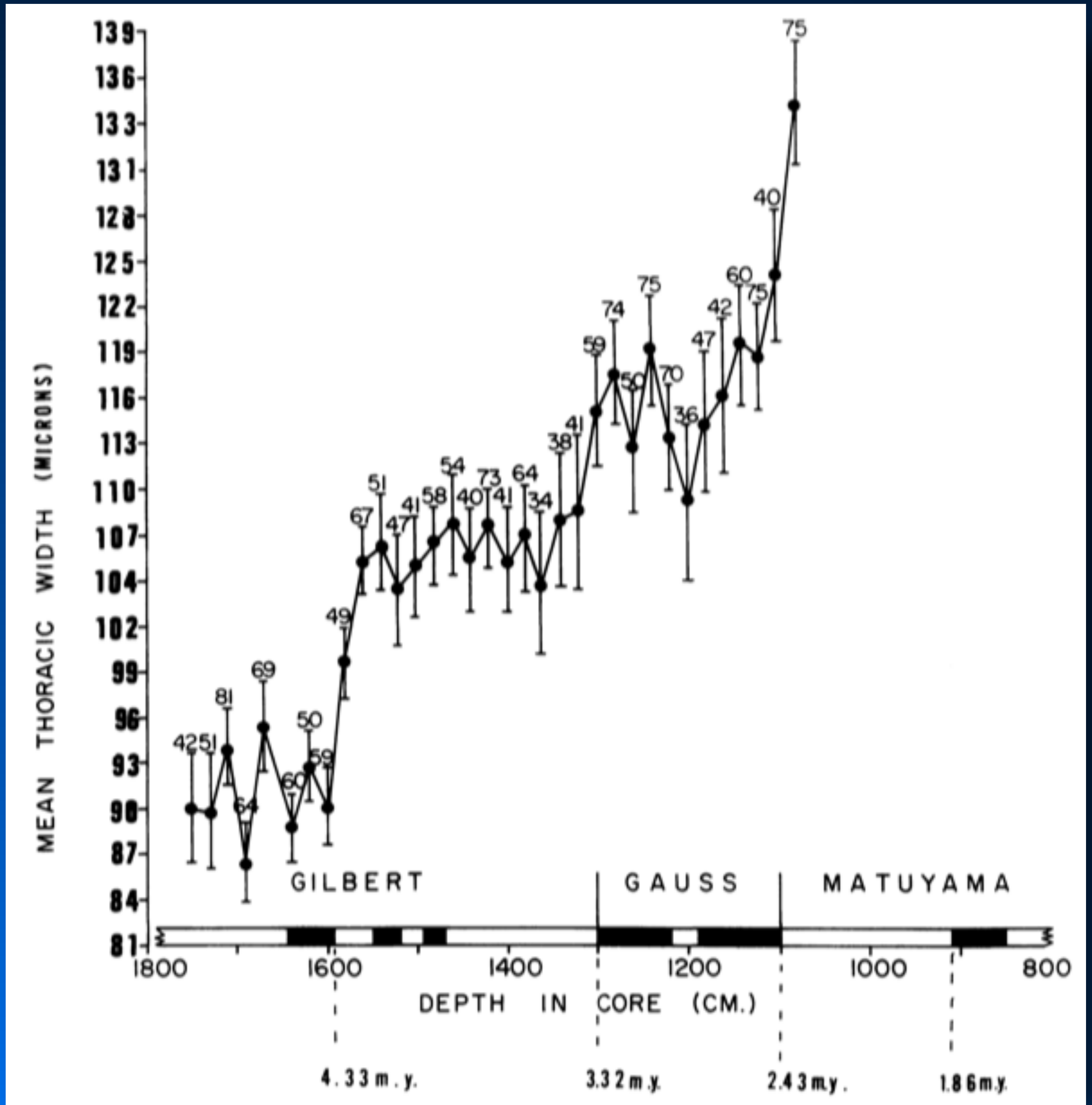



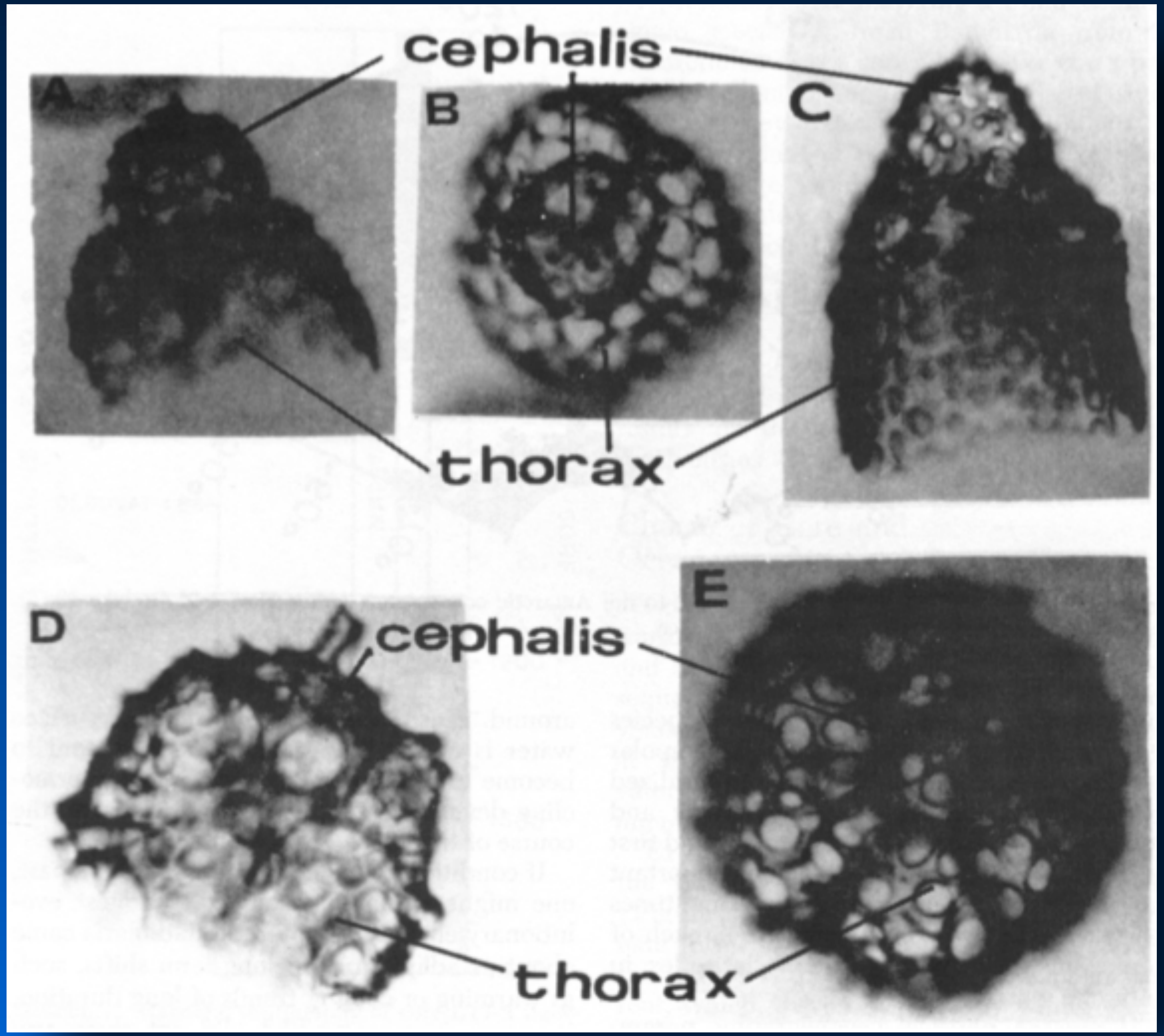

Diagrams from Cheetham (1986)

# Tempos & Modes of Macroevolution

## Evidence Against Punctuated Equilibria

*Pseudocubus vema*



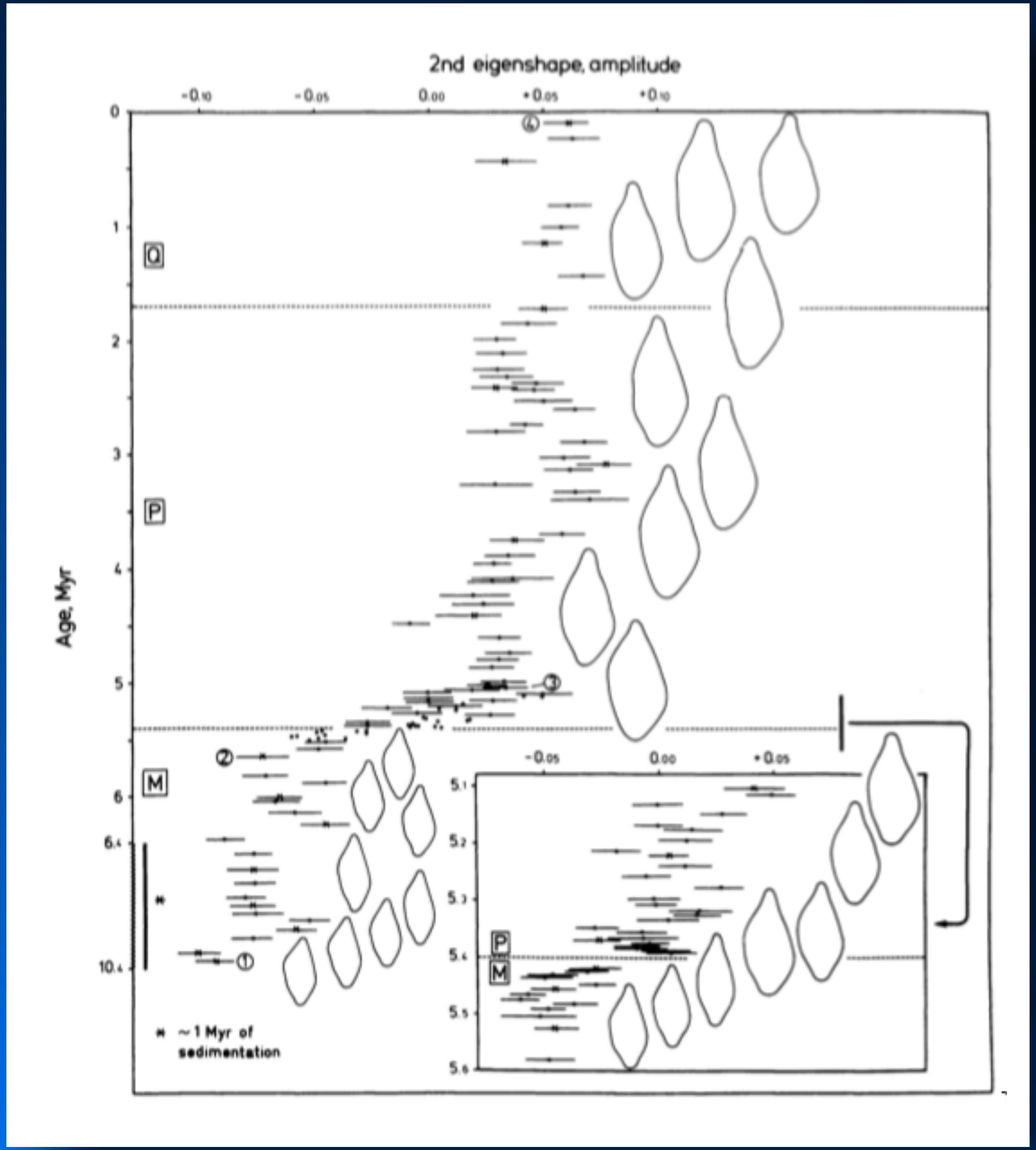




Diagrams from Kellogg (1975)

# Tempos & Modes of Macroevolution

## Evidence For Punctuated Equilibria

*Globotoralia plesiotumida ➛ tumida*




*Globotoralia tumida*

*Globotoralia plesiotumida*

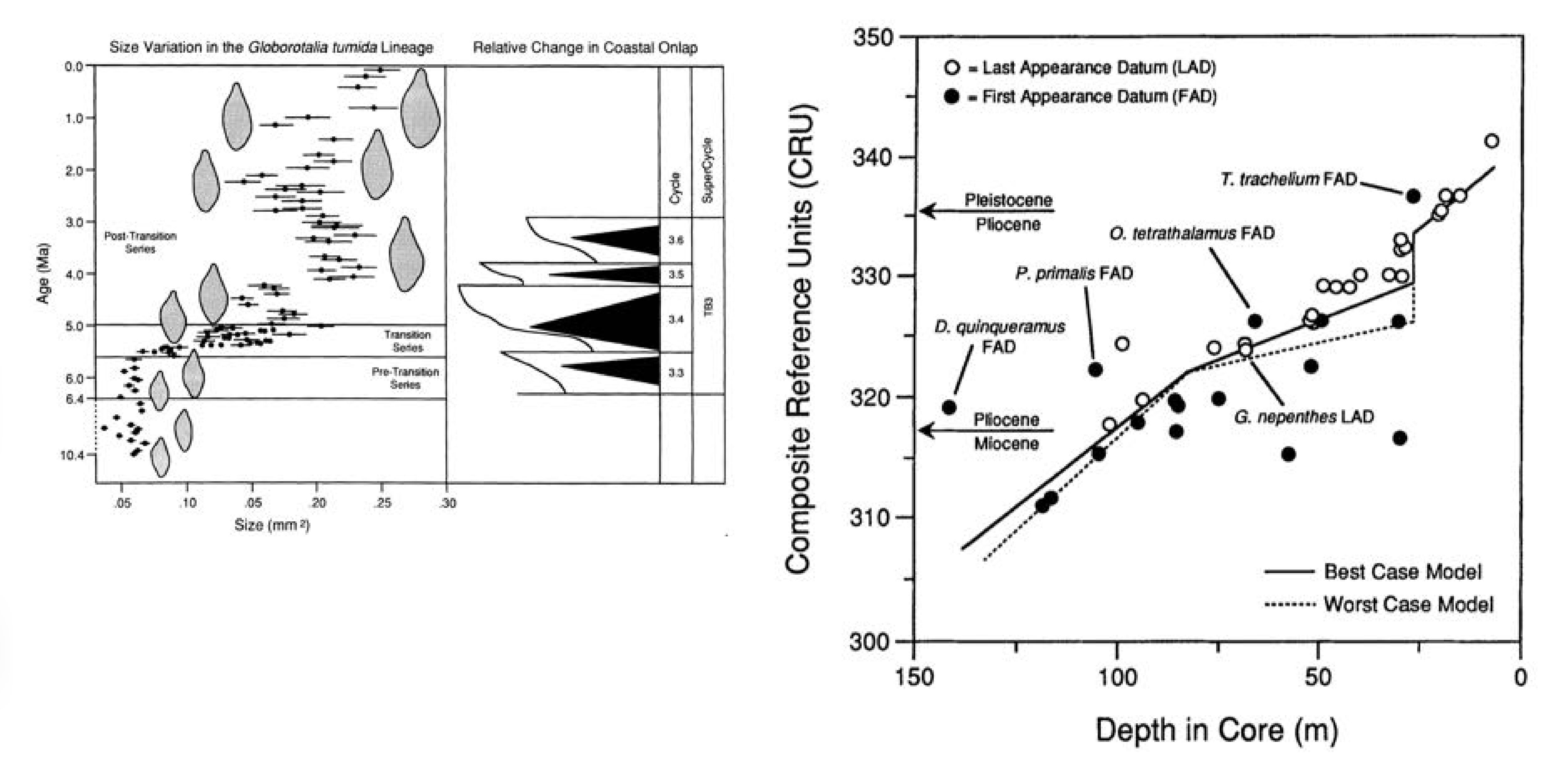
Diagrams from Malmgren et al. (1983)

# Tempos & Modes of Macroevolution

## Evidence Against Punctuated Equilibria

*Globotoralia plesiotumida* ➛ *tumida*

Note that the species transition takes place during a rapid eustatic sea-level rise, that would be expected to results in stratigraphic condensation in deep-sea sediment accumulation patterns. This source of bias in the stratigraphic record would have the effect of inducing an apparent discontinuity in the morphological log of test outline shape in a manner that mimics an apparent rapid morphological transition.



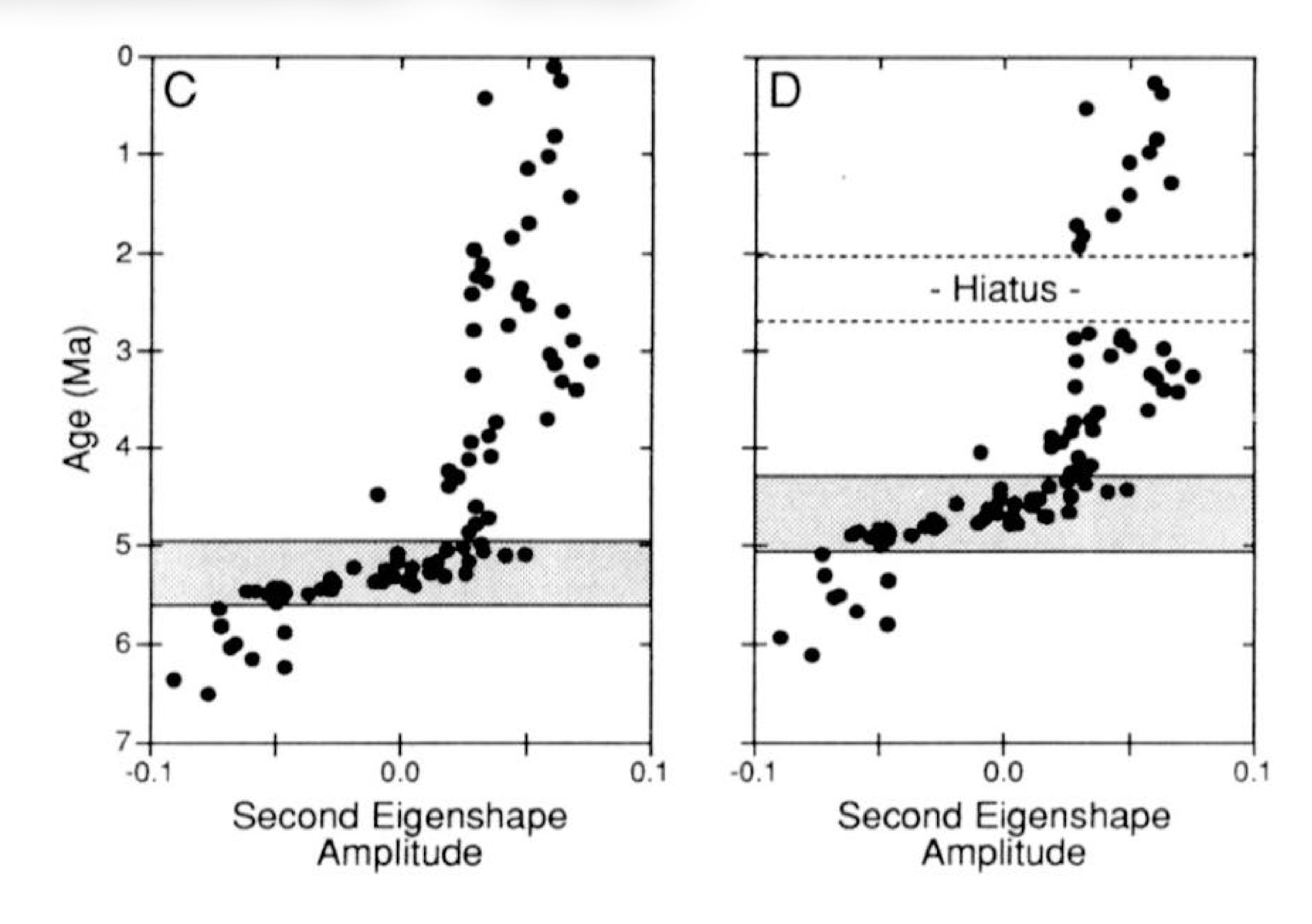

Diagrams from MacLeod (1991)

# Tempos & Modes of Macroevolution

## Evidence Against Punctuated Equilibria

*Globotoralia plesiotumida ➛ tumida*

When the DSDP Site 214 stratigraphic record is corrected for variations in rock accumulation rates and the presence of a hiatus in the deep-sea record, the “punctuated” part of the “punctuated anagenesis” pattern is diminished substantially, to the point where it’s existence is questionable relative to the null hypothesis speciation via ordinary, microevolutionary gradualism.




Diagrams from MacLeod (1991)