ABOUT CAUSATION
CASES OF EVOLUTIONARY CONTINGENCY

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"We may define a cause to be **an object followed by another, and where all the objects, similar to the first, are followed by objects similar to the second**. Or, in other words, where, **if the first object had not been, the second never had existed.**" (DAVID HUME, 1748)

Regulatory definition of causality (LAWS)

Counterfactual definition of causality (HISTORY)

Counterfactual theory of causation - David Lewis 1973: "non-actual possible worlds are real concrete entities"

CAUSE: "We think of a cause as something that makes a difference, and the difference it makes must be a difference from what would have happened without it. Had it been absent, its effects — some of them, at least, and usually all — would have been absent as well."

A) Where c and e are two distinct possible events, e causally depends on c if and only if, if c were to occur e would occur; and if c were not to occur e would not occur.

B) Where c and e are two distinct actual events, e causally depends on c if and only if, if c were not to occur e would not occur.

C) Where c and e are distinct actual events, e causally depends on c if and only if, if c were not occurred, the chance of e's occurring would be much less than its actual chance

EVOLUTIONARY BIOLOGY AS SPECIAL SCIENCE

PROXIMATE CAUSES
(immediate physiological and mechanical factors; how eye works)

+

ULTIMATE CAUSES
(evolutionary forces acting on traits; how eye evolved)

Ernst Mayr, 1997

A problem with deep roots in western Natural Philosophy

The origins of natural design

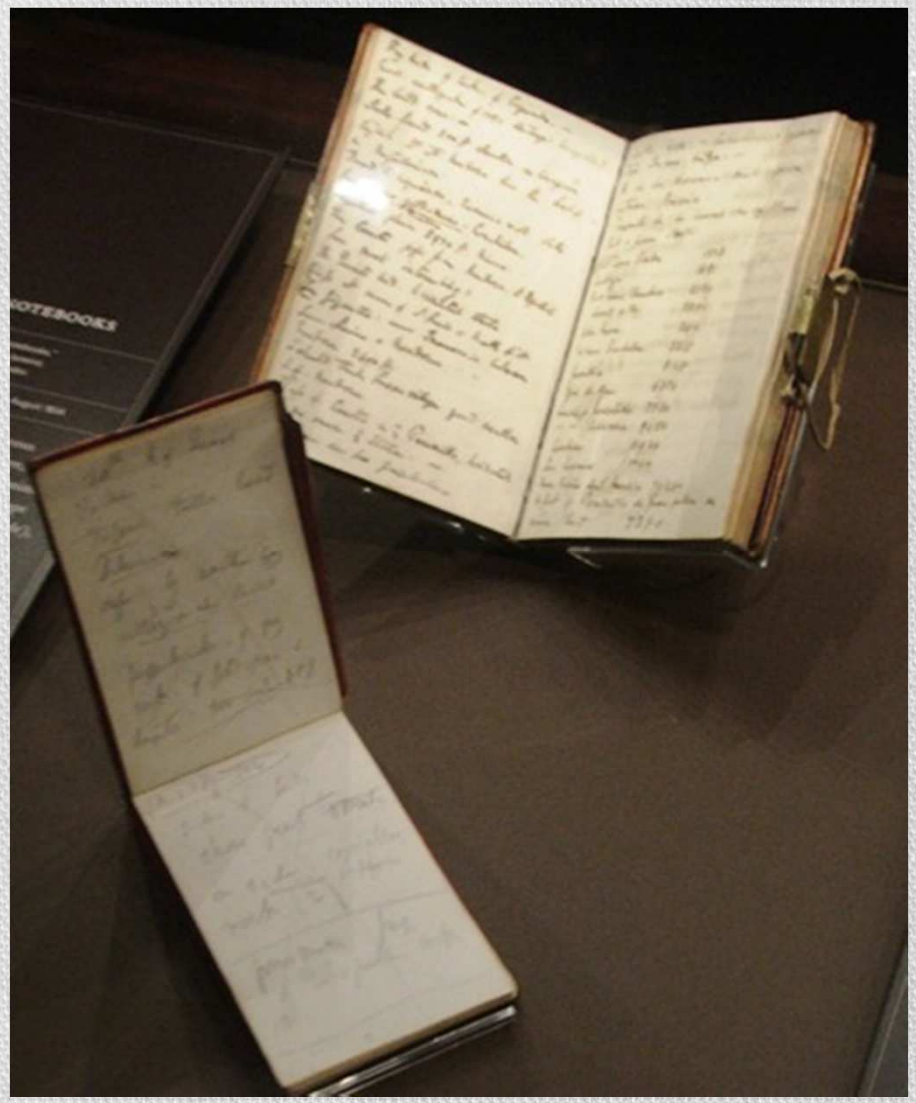
↓

The origins of particularly complex and perfect organs (analogy with artifacts)

"There cannot be design without a designer; contrivance, without a contriver; order, without choice" – **INTENTIONAL CAUSATION**

Young Darwin impressed by the descriptions of "<u>adaptations</u>"

WILLIAM PALEY, Natural Theology, 1802



Charles Darwin's

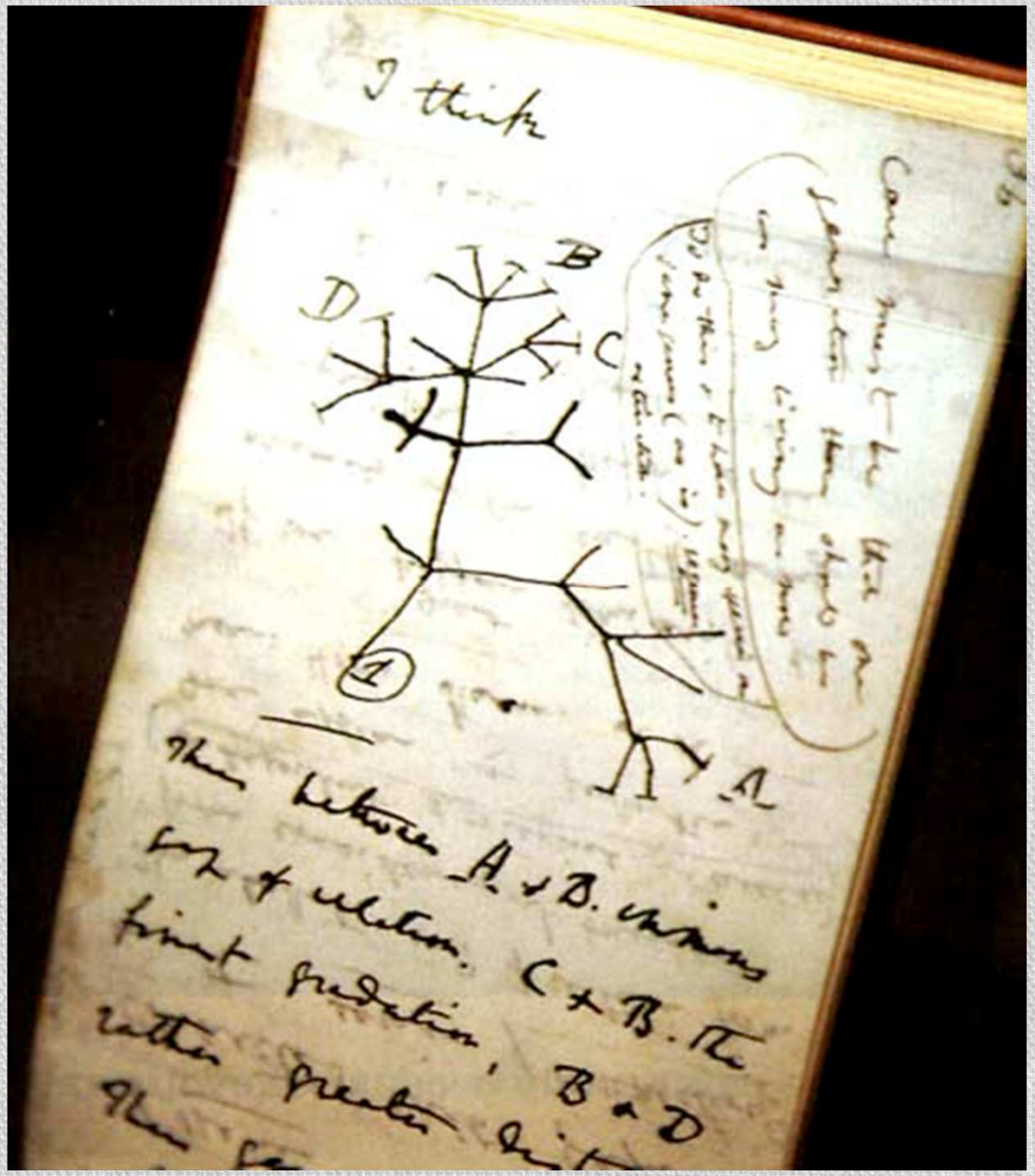
Transmutation Notebooks
(1836-1844)

SOME DOUBTS…

Imperfection: "When one sees nipple on man's breast, one does not say some use. So with useless wings under elytra of beetles, born from beetles with wings and modified. If simple creation, surely would have been born without them" (Notebook B, Sept. 1837)

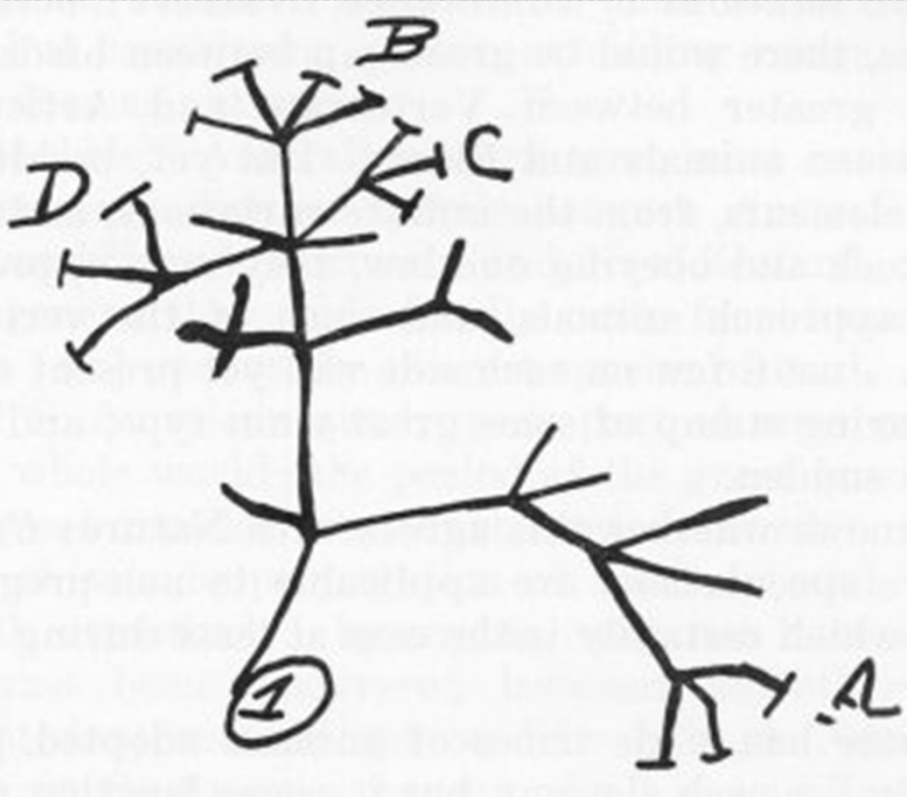
Evolution is not superiority: "It is absurd to talk of one animal being higher than another. We consider those, where the cerebral structure, or intellectual faculties, most developed, as highest. A bee doubtless would when the instincts were" (Notebook B, Sept. 1837)

Simple and sublime: "Astronomers might formerly have said that God ordered each planet to move in its particular destiny. In same manner God orders each animal created with certain form in certain country, but how much more simple and sublime power let attraction act **according to certain laws such are inevitable consequences**… let animal be created, then by the fixed laws of generation, such will be their successors" (ibid. Oct. 1837)



Notebook B, July 1837

I think…



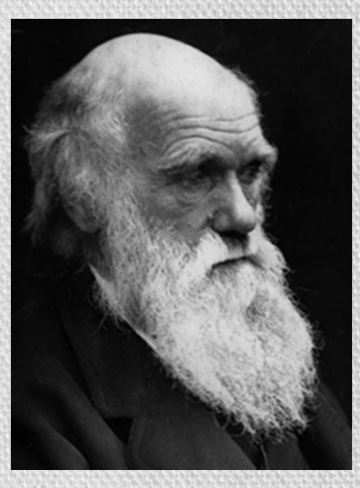
Common ancestors

"The tree of life should perhaps be called the coral of life, base of branches dead; so that passages cannot be seen. … Between genera immens gap of relation, or the finest gradation, or rather greater distinction" (CD, Notebook B, July 1837)

Obs. 1: Exponential growth of populations

Obs. 2: The balance of populations

Obs. 3: Limited resources



Ded. 1: Struggle for existence

Obs. 4: Individual diversity

Obs. 5: Heredity of a part of the individual variation

Obs. 6: Variation is not externally directed

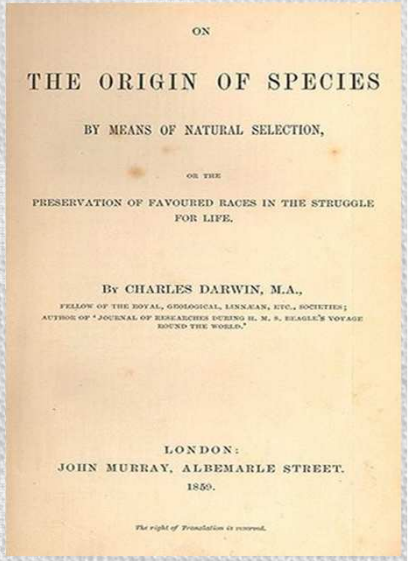
Ded. 2: Differential survival

Ded. 3: Differential reproductive success, over generations: change within populations.

Ded. 4: (Principle of divergence) Descent with Modifications

- Is natural selection a «UNIVERSAL LAW» like those we know in physics?
- Natural selection makes some effects more PROBABLE than others

Risky predictions…


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.,

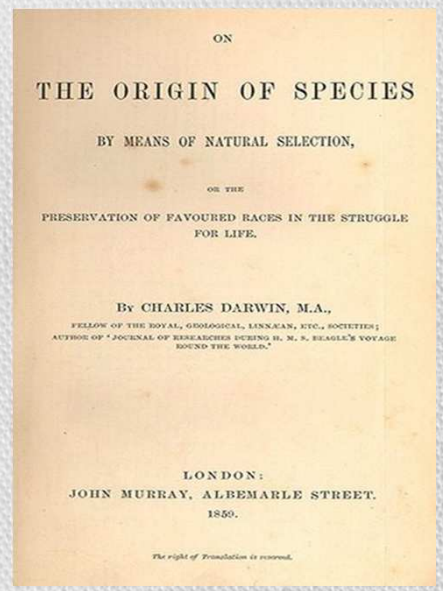
FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

The right of Translation is reserved.

"To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree." (CD, *Origin*, Sixth Edition, 1872)

"If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down" (p. 146)



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Non-adaptations

«Le suture nel cranio dei giovani mammiferi sono state prospettate come un bell'adattamento per facilitare il parto, e senza dubbio esse l'agevolano, o possono essere indispensabili per quest'atto; ma poiché le suture si riscontrano anche nel cranio di giovani uccelli e rettili, che hanno soltanto da uscire da un uovo rotto, possiamo inferire che questa struttura è sorta dalle leggi della crescita (*laws of growth*) ed è stata utilizzata per il parto negli animali superiori». (p. 255)

- Ancora, dalla discendenza comune ipotesi selettive.
- Sorgenti di strutture non adattative, in seguito convertite a usi funzionali, in DW: variazioni spontanee; tendenza alla reversione; effetti delle "complesse leggi della crescita"; correlazioni di sviluppo; compensazioni; variazioni omologhe; pressione esercitata da una parte su un'altra; selezione sessuale di caratteri utili a un sesso ma condivisi anche dall'altro sesso benché inutili (p. 255).

DARWIN:

continuity in differential reproductive success, not in the same function

- **CURRENT USE not always => HISTORICAL ORIGIN**

- **SUB-OPTIMALITY of adaptation**

"Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it comes into competition. And we see that this is the standard of perfection attained under nature. Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature" (p. 163)

"I am convinced that **Natural Selection has been the most important, but not the exclusive, means of modification**" (p. 4)

So, NATURAL SELECTION = A PATTERN (the most important) AMONG OTHERS

“QUIRKY FUNCTIONAL SHIFT”

Exaptation: a missing term in the science of form

(S.J. Gould, E. Vrba, 1982)

APTATION: any features now contributing to fitness

- **AD-APTATION**: a feature directly crafted for a current utility by natural selection

- **EX-APTATION**: a feature coopted for a current utility following an origin for a different function, or for not function at all.

“Exaptation”: character useful (*aptus*) as a consequence of (*ex*) its form

1941 - 2002

"To paraphrase Mr. Huxley in a famous context, I am prepared to go to the stake for exaptation; for this new term stands in important contrast with adaptation, defining a distinction at the heart of evolutionary theory, and also plugging an embarassing hole in our previous lexicon for basic processes in the history of life."

(S.J. Gould, "The Structure of Evolutionary Theory", 2002, p. 1234)

A NEW TAXONOMY OF FITNESS

Process	*Character*	*Usage*
Natural Selection shapes the character for a current use	**Adaptation**	Function
A character, previously shaped by natural selection for a particular function (an adaptation), is coopted for a new use	**Exaptation (by cooptation)**	Effect
A character whose origin cannot be ascribed to the direct action of Natural Selection (a non-aptation), is coopted for a current use	**Exaptation (by nonaptation)**	Effect

TAXONOMY OF THE EXAPTIVE POOL

as structural basis of "evolvability" in life's history

(S.J. Gould, 2002)

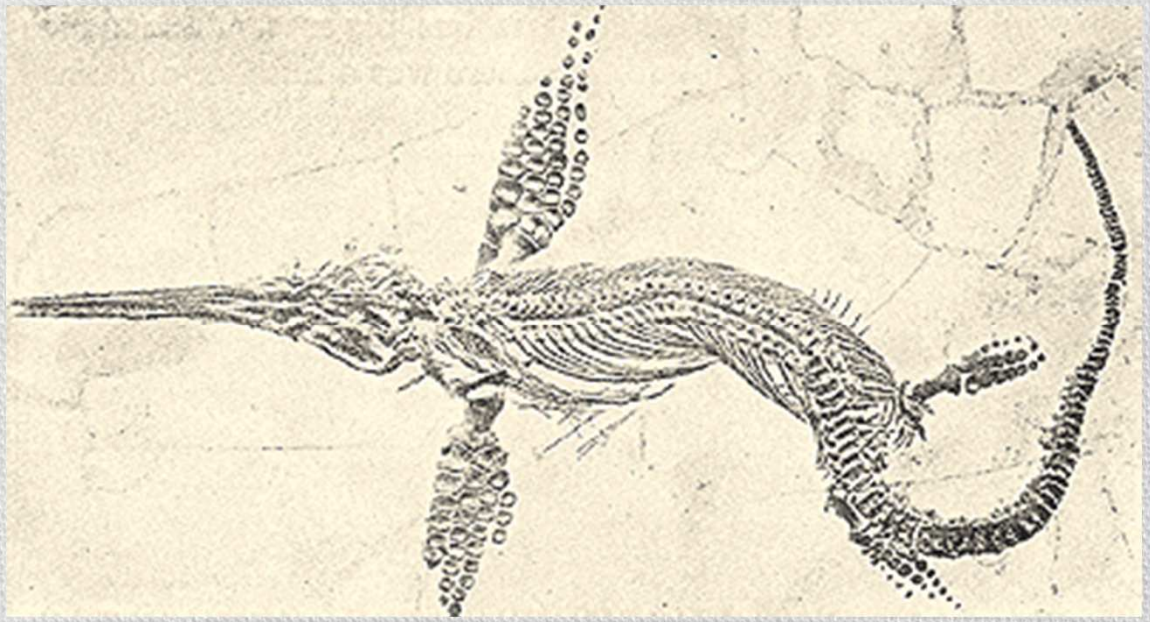
A – Inherent potentials (unexploited)

B – Available things ("spandrels")

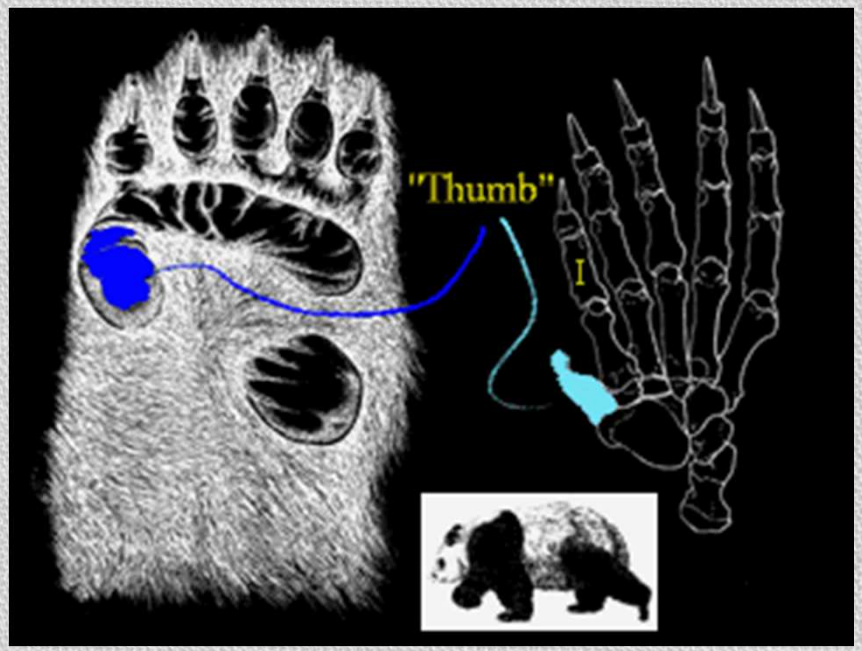
B1) As architectural consequences (structural and non-adaptive origin)

B2) As historical unemployments (historical, non-adaptive origin) (*ex. vestigia*)

B3) As invisible introductions (historical, non-adaptive origin) (*ex. neutral drifts, founder effects*)



Ichthyosaurus



The Five Percent of a Wing Problem - 2007

Archaeopteryx lithographica

Solnhofen, 1861
(Richard Owen)

ADAPTIVE STORIES?

Protowings? Transitional stages?

Dinosaurs with plumage?

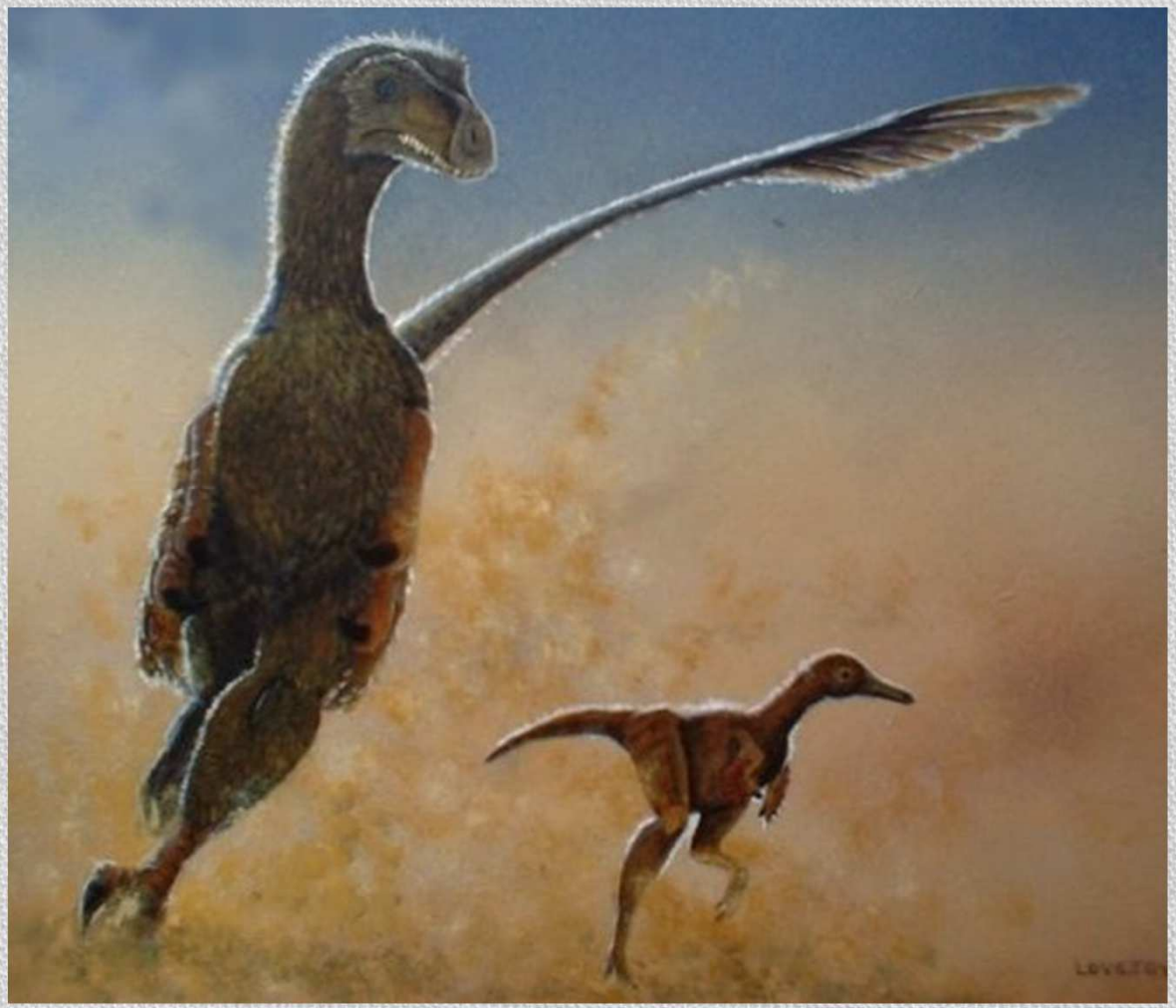
1996-2006: AMNH of NY

A) **Arboreal Theory** (for gliding in tree-dwelling ancestors)

B) **Cursorial Theory** (from running terrestrial dinosaurs)

C) **Wing-assisted incline running** in avian ancestors (Dial, Randall, Dial, *BioScience*, 56, n. 5, May 2006)

Anyway: **Exaptation (type 1) of avian flight**



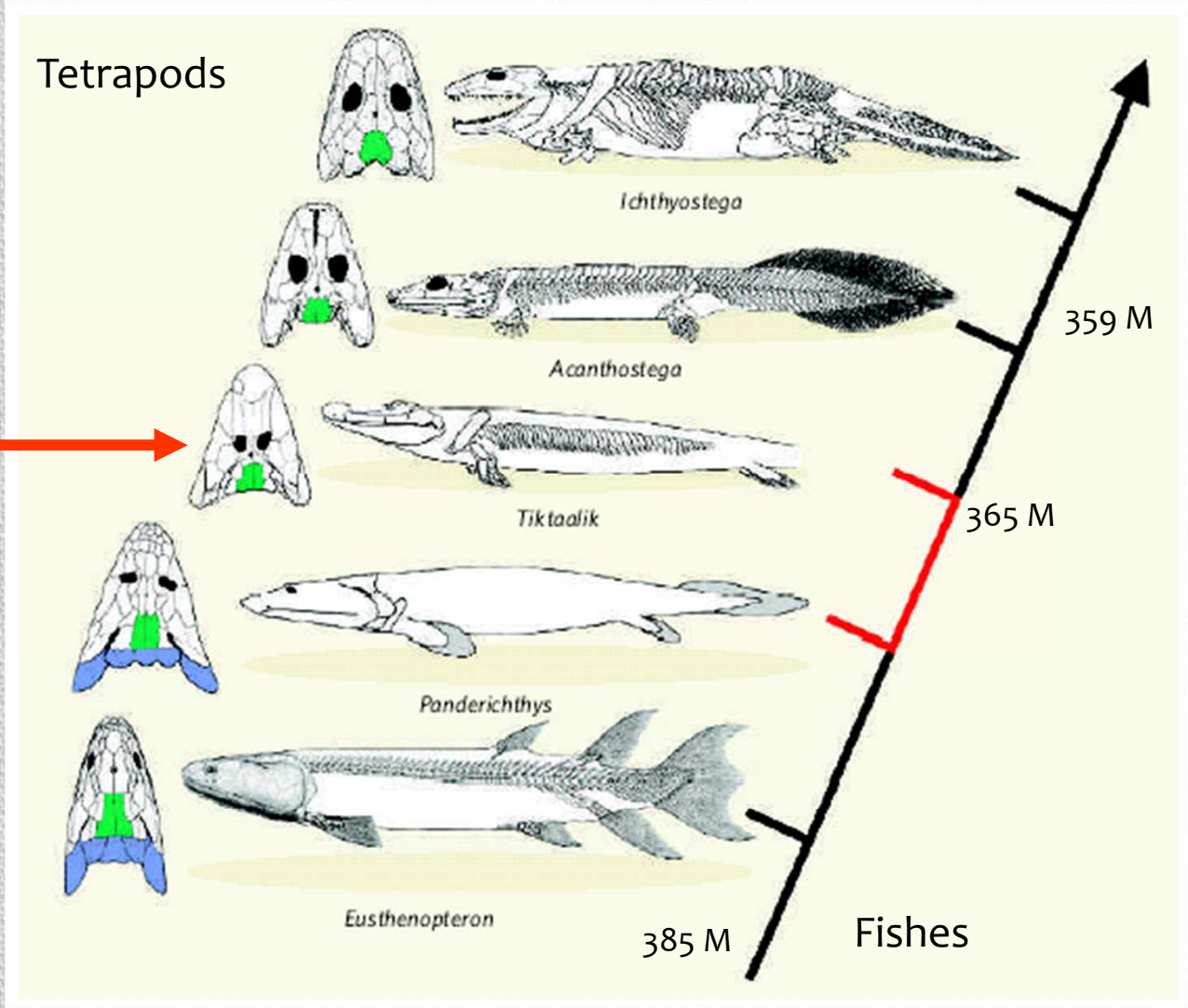
Velociraptor mongoliensis with Mononykus olecranus

"A firm step from water to land" (*Nature*, 440, April 2006)

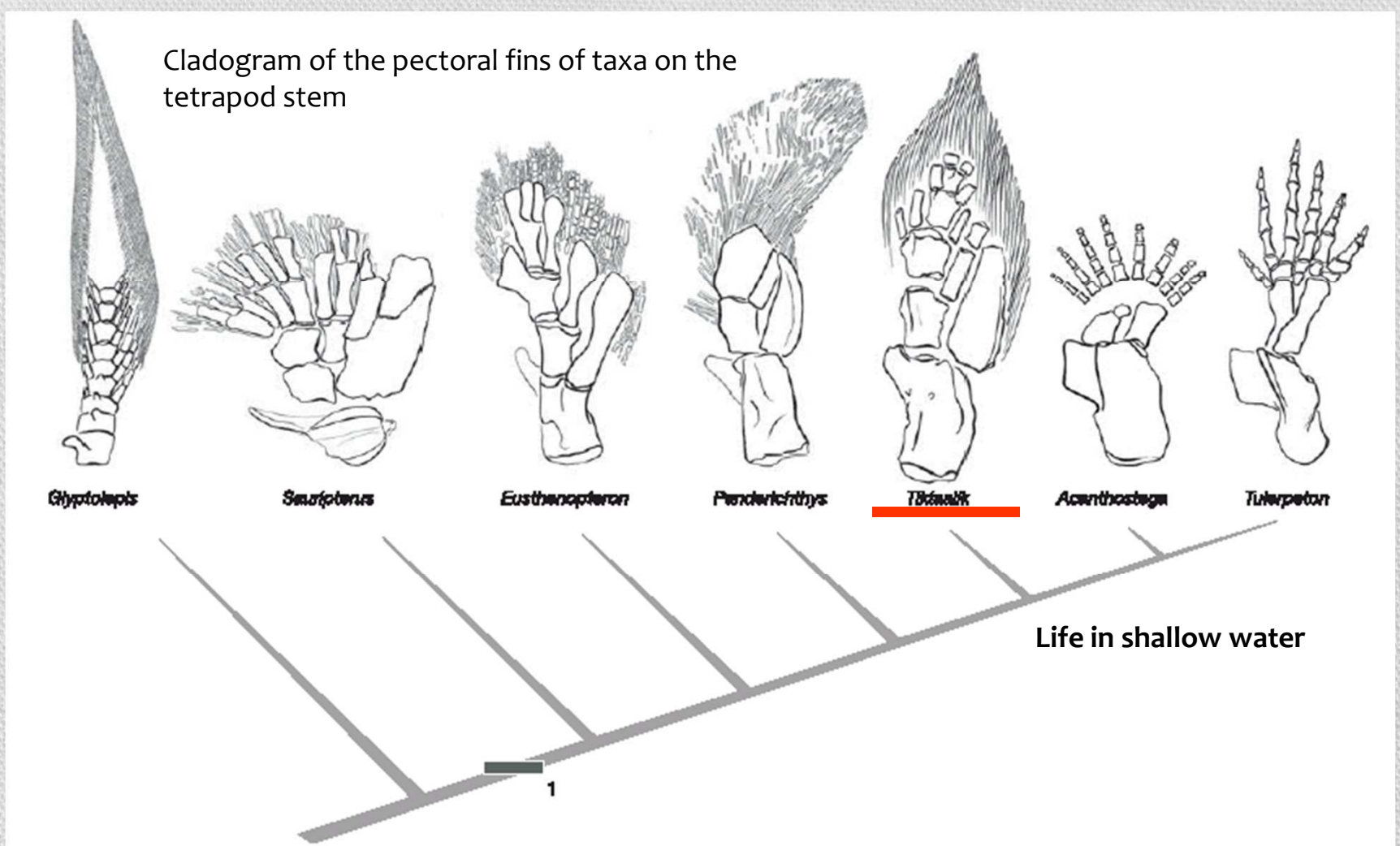
Tiktaalik roseae – Ellesmere Island, Nunavut, Arctic Canada (Shubin, Daeschler, Jenkins, *Nature*, 440, 2006)

Single intermediate fossil? Missing link?

What is the right pattern for vertebrate transition from water to land?



Classic picture Devonian–Carboniferous: LINEAR ANAGENESIS?



- **Multiple adaptive solutions** (different combinations of "retained" and "modern" characters)

- **Exaptation fins-limbs**

- **Not always the present is the key for the past (Henry Gee)**

Functional change by cooptation

The revolution in understanding the morphological transformation from fin-bearing to limb-bearing tetrapods began with renewed expeditions to East Greenland that recovered complete specimens of *Acanthostega* (Clack 2002). This material revealed an animal less than a meter in length with a series of characters betraying its aquatic habit: a well-developed gill skeleton [Coates & Clack 1991; a gill skeleton has subsequently been reported in *Ichthyostega* (Clack et al. 2003)], paddle-like limbs bearing eight digits each (Coates 1996), and a tail with fin rays and radials (Coates 1996). These finds challenged the established notion that limbs evolved for terrestrial locomotion, and instead placed their origin squarely within an aquatic environment.

NATURAL SELECTION ACTS ON CONTRAINTS (ONTOGENETIC, HISTORICAL, STRUCTURAL)

doi 10.4436/jass.89015
e-pub ahead of print

JASs Invited Reviews
Journal of Anthropological Sciences
Vol. 89 (2011), pp. 1-15

Exaptation in human evolution: how to test adaptive *vs* exaptive evolutionary hypotheses

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Evol Biol (2012) 39:613–637
DOI 10.1007/s11692-012-9162-y

SYNTHESIS PAPER

Evolutionary Developmental Biology and Human Language Evolution: Constraints on Adaptation

W. Tecumseh Fitch

Received: 2 January 2012 / Accepted: 24 January 2012 / Published online: 7 March 2012

LETTER

doi:10.1038/nature12301

A latent capacity for evolutionary innovation through exaptation in metabolic systems

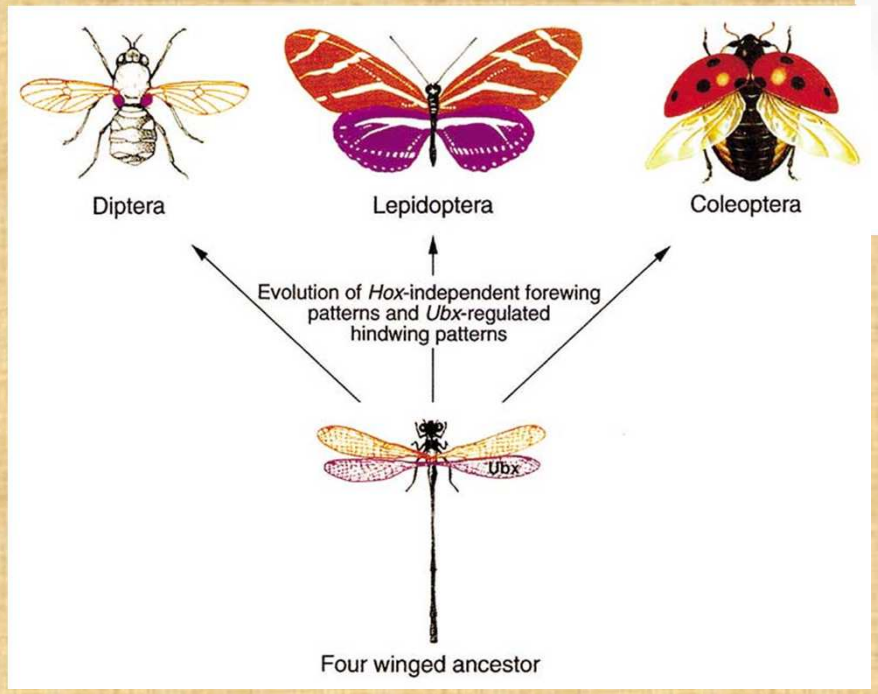
Aditya Barve[1,2] & Andreas Wagner[1,2,3]

EVO-DEVO: HOX-MUTATIONS IN PHYLOGENY

- Same Hox genes for the entire animal kingdom

- Nat. Selection and Dev. Constraints

- Traits without adaptation (structural effects)



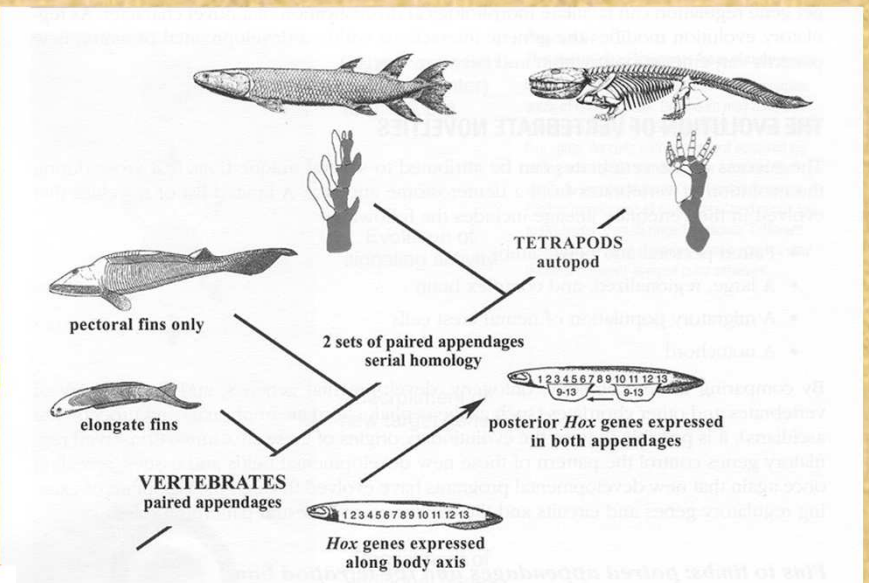


Figure 6.7
Evolution of vertebrate paired appendages

Vertebrate paired appendages evolved in a series of steps. Paired appendages are first encountered in the fossil record as elongate fins extending laterally along the body wall or as paired pectoral fins in jawless fish (shown on basal branches). Jawed fish are characterized by multiple sets of paired appendages that often have a defined fin axis (shown in blue; **top left**). Tetrapods (**top right**) have a distal autopod, with digits branching from a bend in the limb axis. One step in the evolution of serially homologous paired appendages was the co-option of nested patterns of posterior *Hox* genes expression in both sets of paired appendages (**lower right**).

Source: Modified from Shubin N, Tabin C, Carroll S. Nature 1997;388:639–648.

Evolution and bricolage: functional shifts and cooptations

THE PARADOX OF ADAPTATIONISM

"To see natural selection, and the creation of complex design, as the centerpiece of evolutionary theory is to retain the problem that was created by Paley and the theologians and merely to replace their solution to the problem with a naturalistic solution: to retain a focus on the problem of complex design is to adopt naturalism, but only within the framework of natural theology"

(Peter Godrey-Smith, 1999, B&P 14)

Junk DNA and Garbage DNA

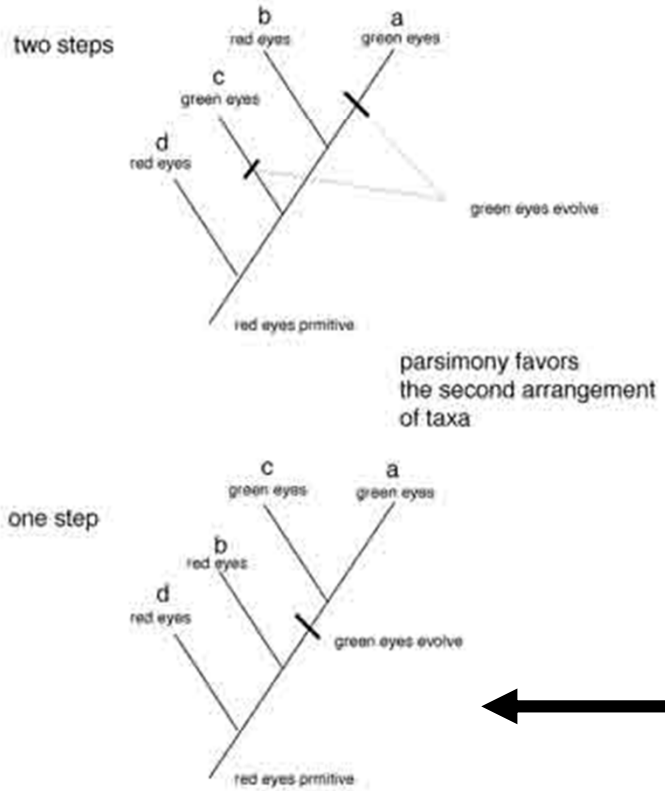
"Some years ago I noticed that there are **two kinds of rubbish** in the world and that most languages have different words to distinguish them. There is the rubbish we keep, which is junk, and the rubbish we throw away, which is garbage. The **excess DNA in our genomes is junk**, and it is there because it is harmless, as well as being useless, and because the molecular processes generating extra DNA outpace those getting rid of it. Were **the extra DNA to become disadvantageous, it would become subject to selection**, just as junk that takes up too much space, or is beginning to smell, is instantly converted to garbage."
(Sydney Brenner, 1998)

The Onion Test

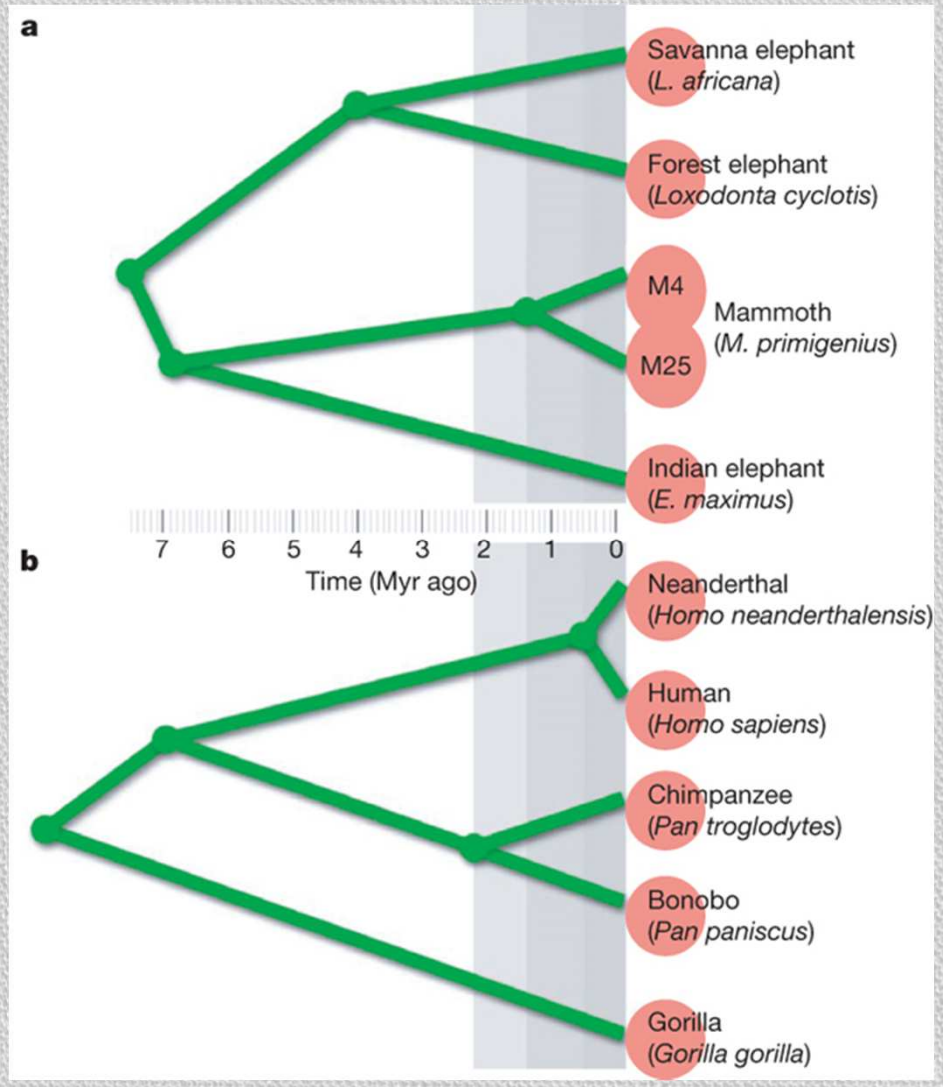
"The onion test is a simple reality check for anyone who thinks they can assign a function to every nucleotide in the human genome. Whatever your proposed functions are, ask yourself this question: Why does an onion need a genome that is about five times larger than ours?"

(T. Ryan Gregory)

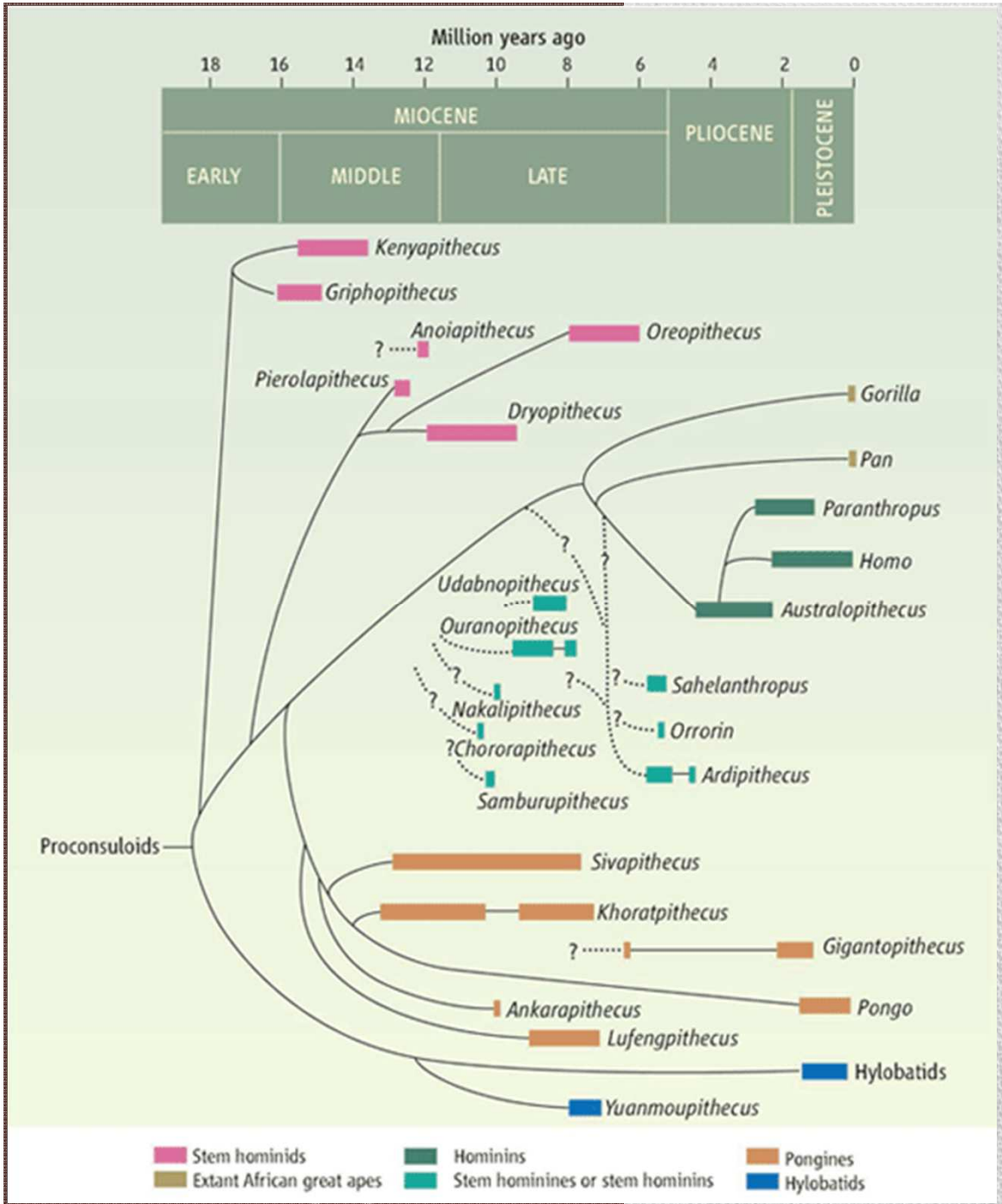
PARSIMONY



Comparison of phylogenies



W Miller *et al. Nature* **456**, 387-390 (2008) doi:10.1038/nature07446

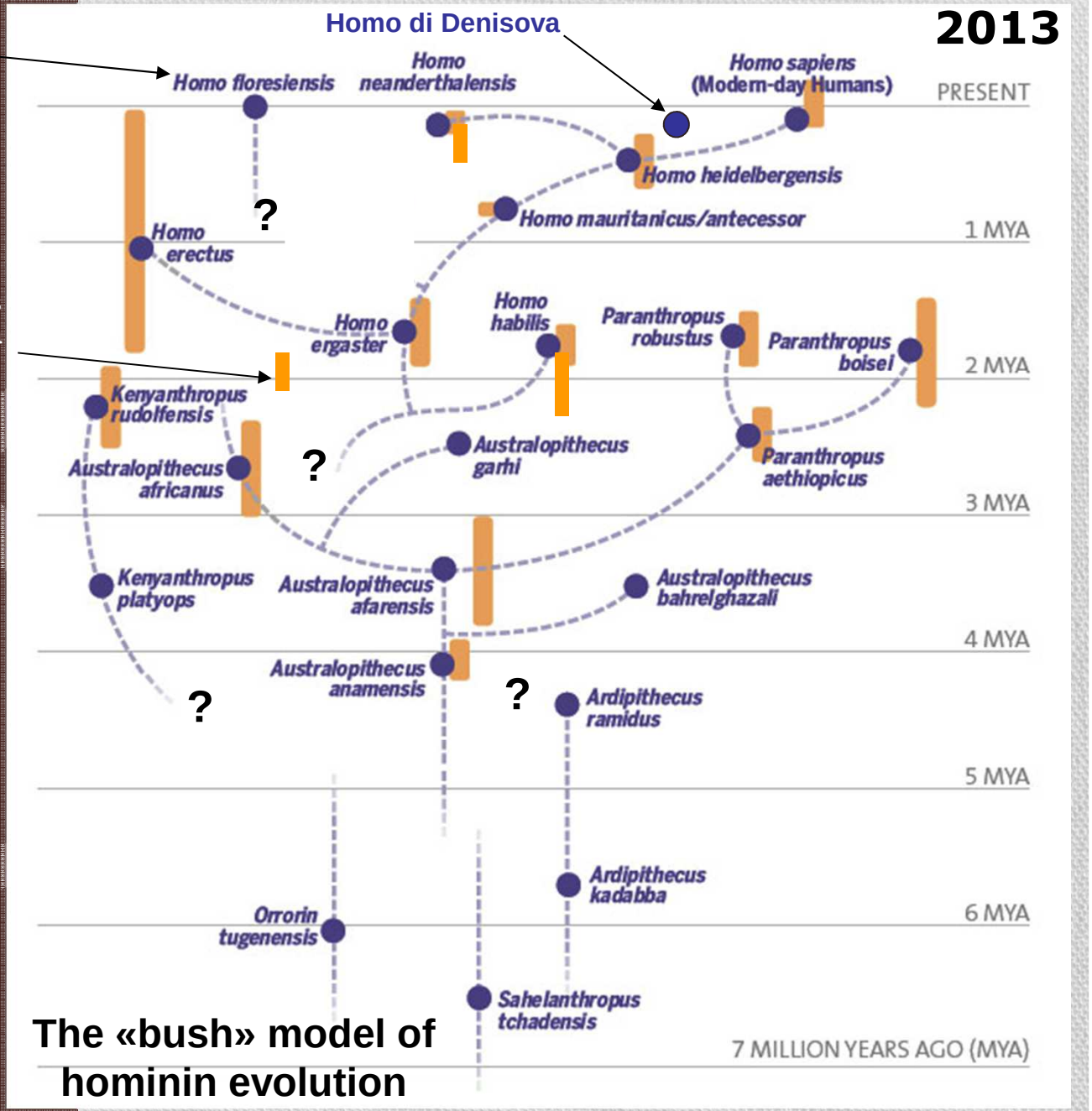


Hominoid relationships.

Schematic representation of the inferred evolutionary relationships between Miocene apes, early hominins, and extant hominoids. Solid gray bars represent the known time range of each genus, thin dark lines are inferred relationships between the genera, and thin dashed lines with "?" denote uncertain relationships.

Terry Harrison , *Apes Among the Tangled Branches of Human Origins*, Science 2010: Vol. 327. no. 5965, pp. 532 – 534.

- Homologies and analogies
- Speciations and adaptive uniqueness
- Biogeography
- Brain growth (trend)
- Vocal trait



The «bush» model of hominin evolution

GENETIC DRIFT: random changes in genic frequencies due to population structure

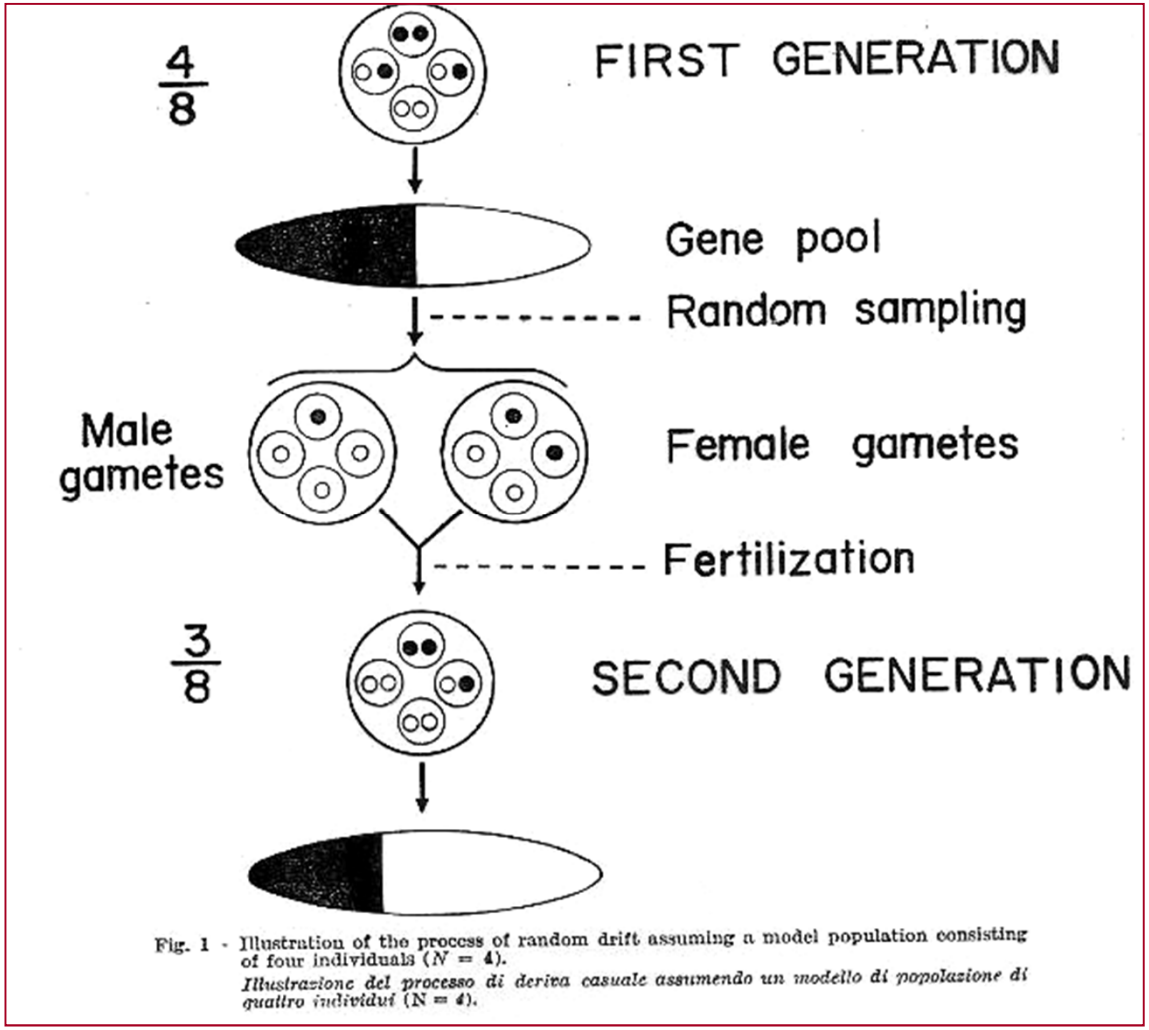
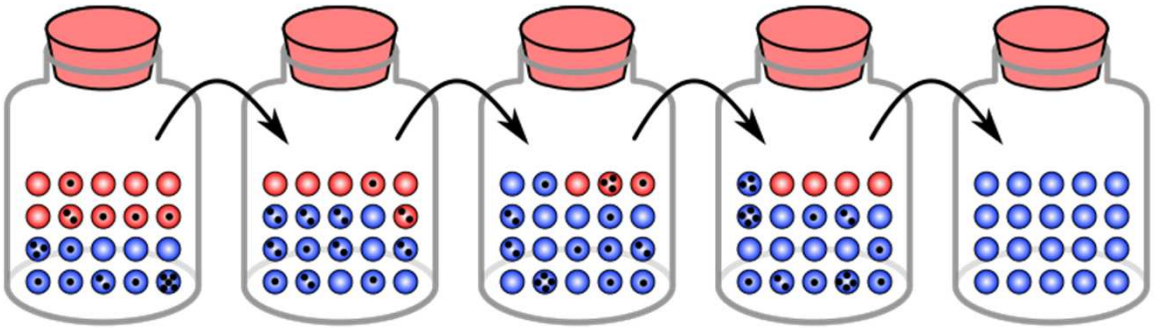


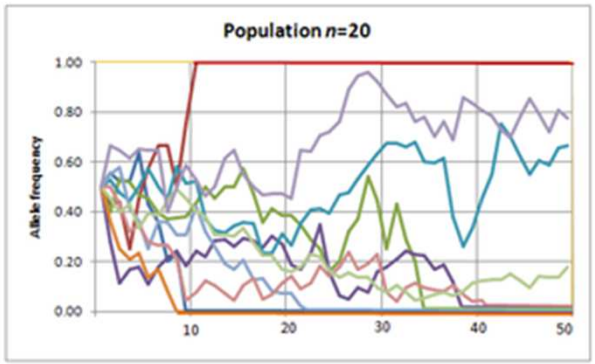
Fig. 1 - Illustration of the process of random drift assuming a model population consisting of four individuals ($N = 4$).
Illustrazione del processo di deriva casuale assumendo un modello di popolazione di quattro individui ($N = 4$).

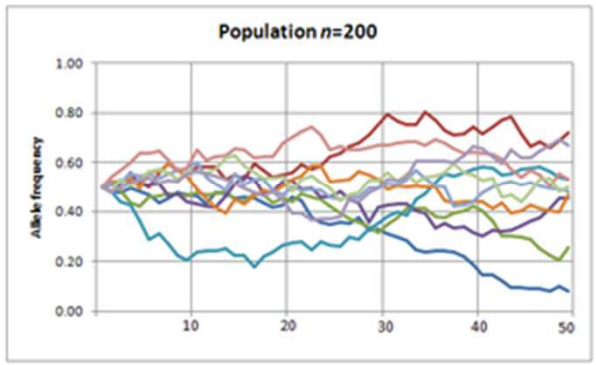
Drift depends on population size

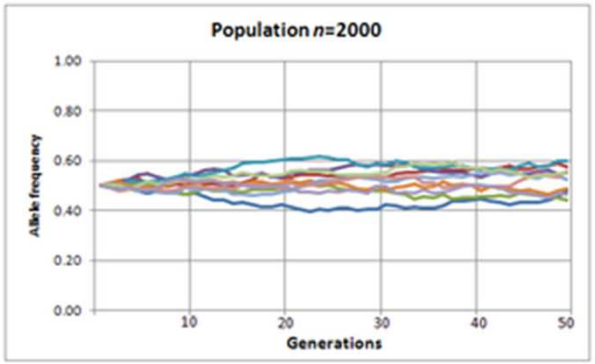
Kimura, *Scientia*, 704

Small population = deeper fluctuations

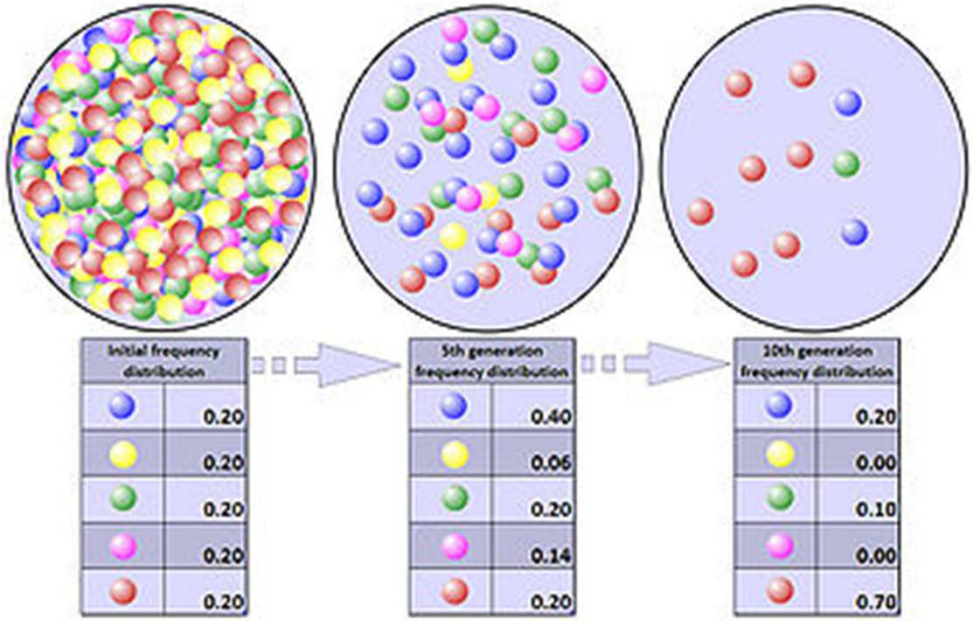




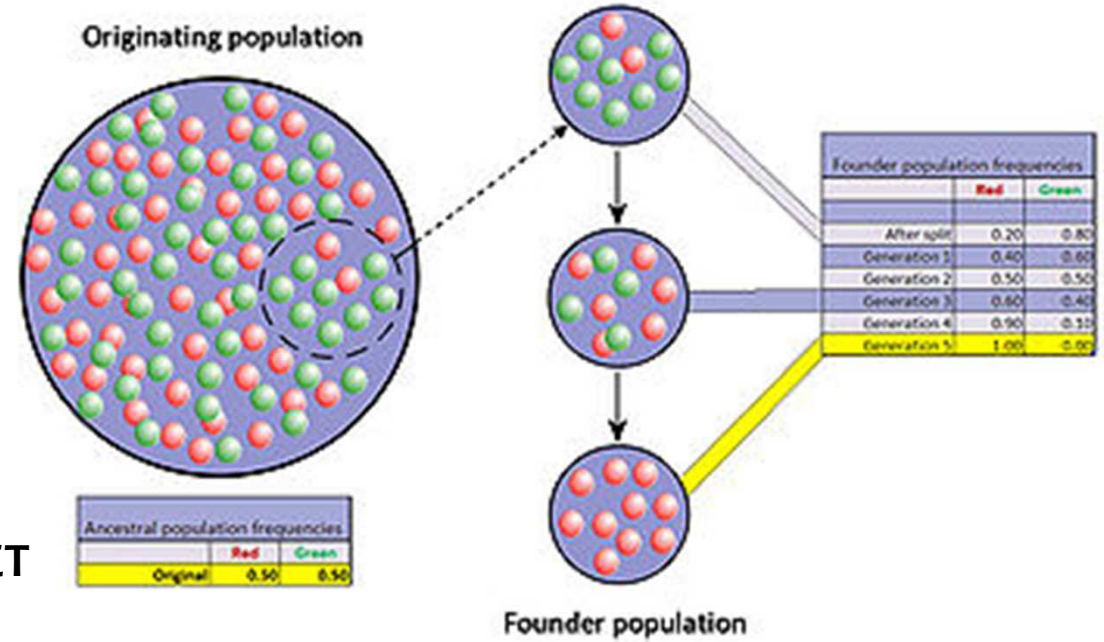




BOTTLENECK



FOUNDER EFFECT



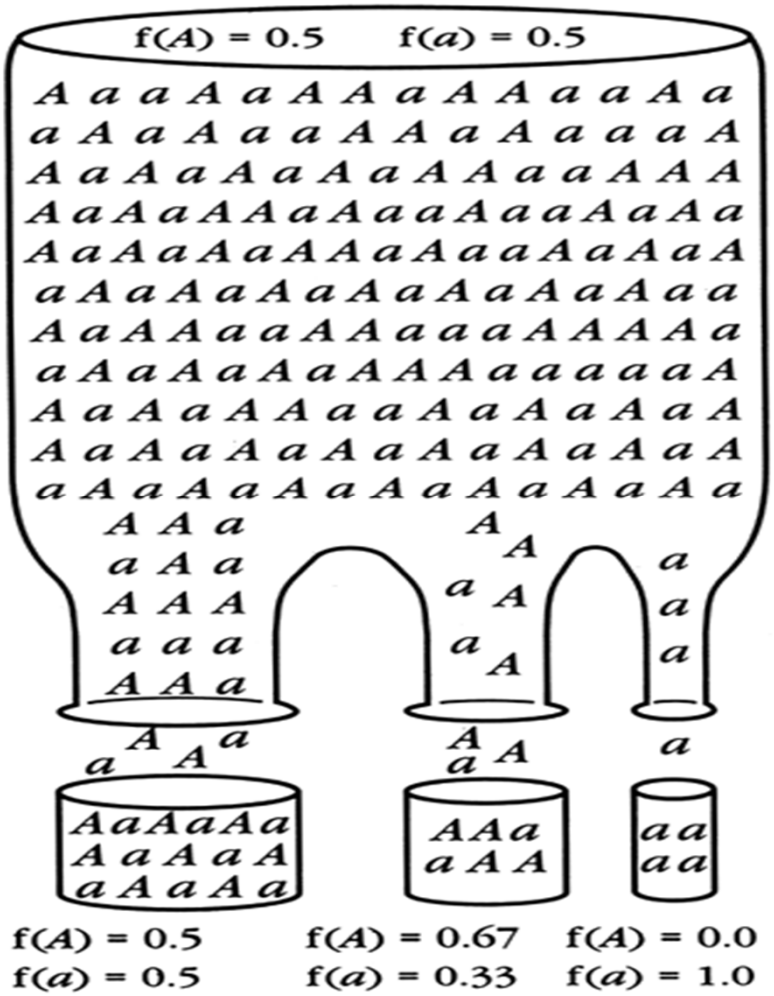
The outcomes of the genetic drift may be:

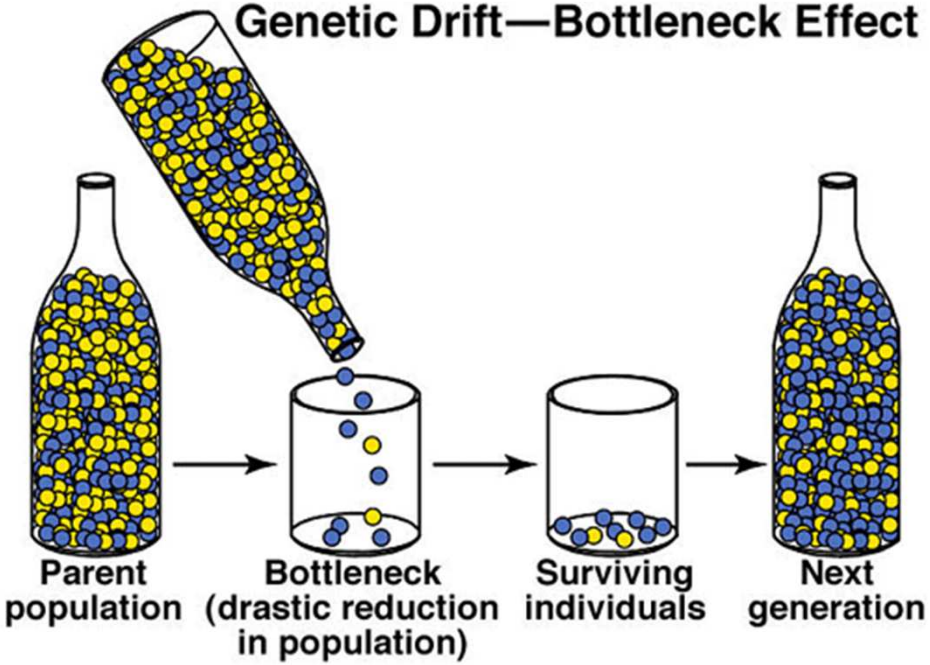
-1) The loss or fixation of alleles *independently from their selective value*

- 2) A loss of genetic variability, different from one small population to another

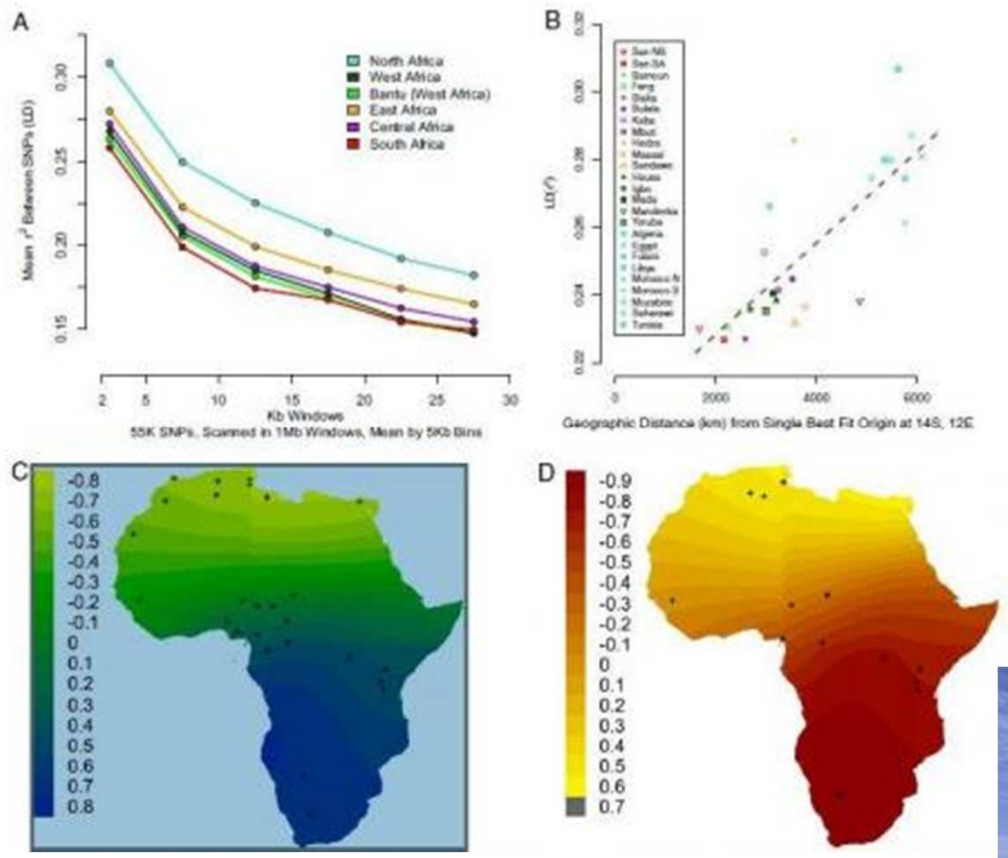
Bottleneck events

in human evolution





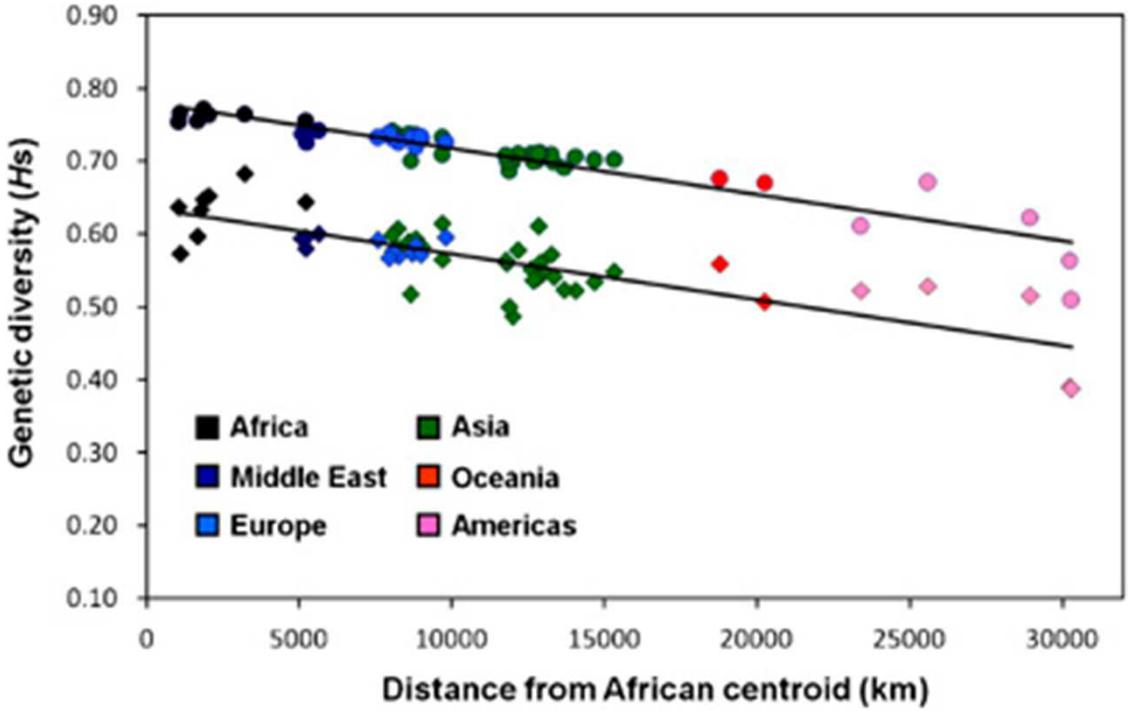
A – Genetic diversity has a maximum



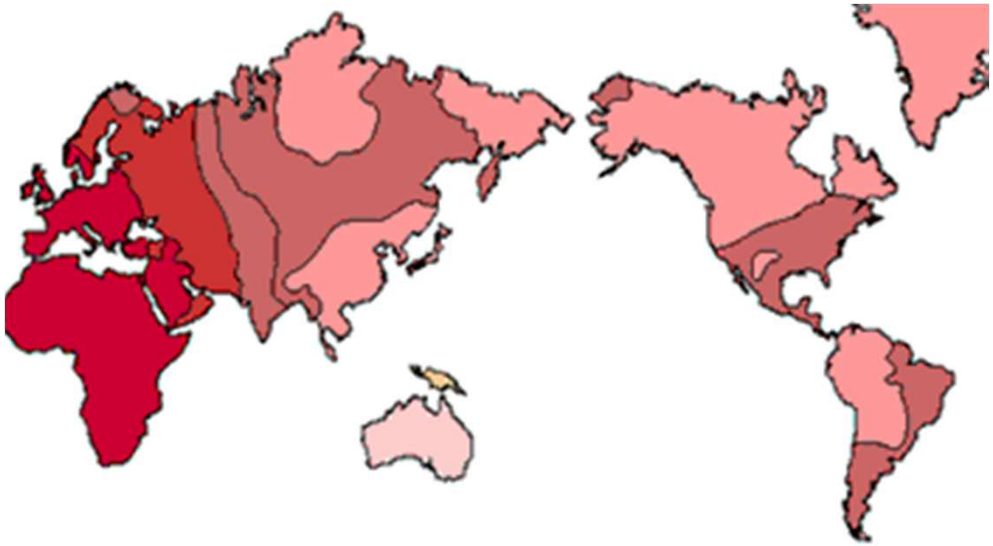
Henn et alii, "Hunter-gatherer genomic diversity suggests a southern African origin for modern humans", PNAS, March 2011, vol. 108, n. 13.

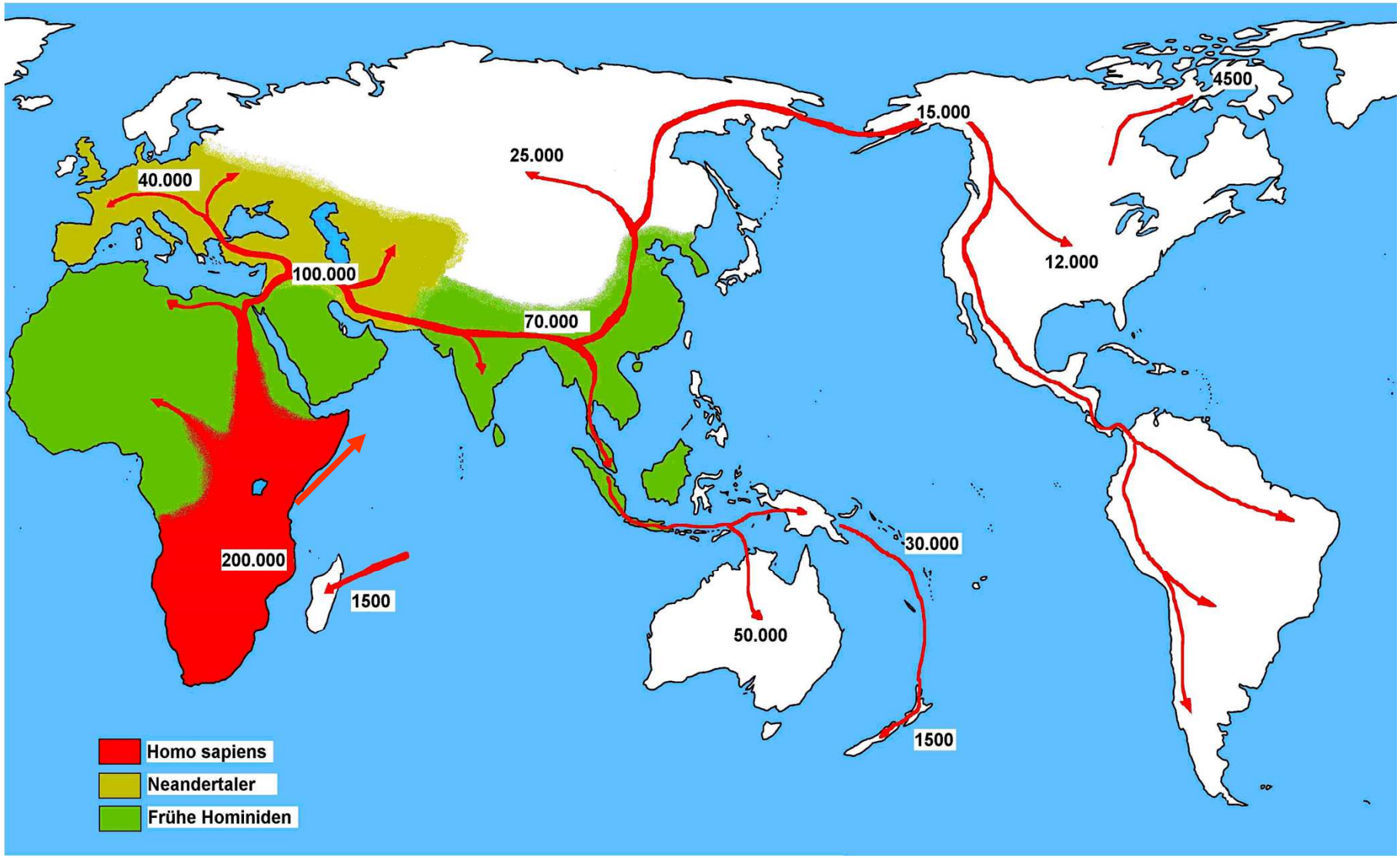
"African hunter-gatherer populations, with a maximum in southern Africa, continue to maintain the highest levels of genetic diversity in the world".

B – Genetic diversity decreases with distance from Africa



Ramachandran et alii, "Support from the relationship of genetic and geographic distance in human populations for a serial founder effect originating in Africa", PNAS, 2005, 102, n. 44





RANDOM GENETIC PROCESSES PRODUCE VERY PREDICTABLE AND LAW-LIKE PATTERNS IN EVOLUTION!

Human expansion *out of Africa* has been accompained by a series of founder effects

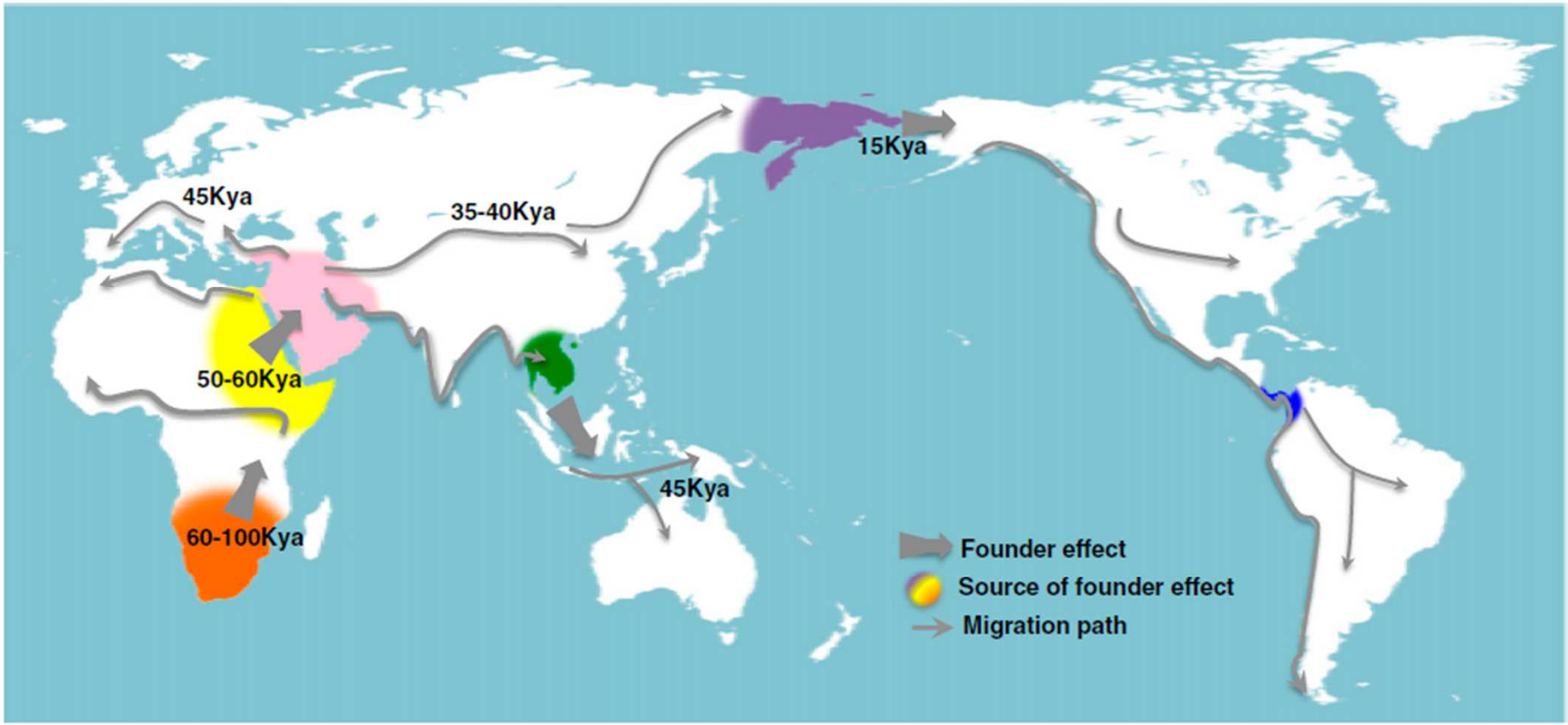


Fig. 1. Ancient dispersal patterns of modern humans during the past 100,000 y. This map highlights demic events that began with a source population in southern Africa 60 to 100 kya and conclude with the settlement of South America approximately 12 to 14 kya. Wide arrows indicate major founder events during the demographic expansion into different continental regions. Colored arcs indicate the putative source for each of these founder events. Thin arrows indicate potential migration paths. Many additional migrations occurred during the Holocene (11).

B. M. Henna, L. L. Cavalli-Sforza, & M. W. Feldman The great human expansion
***PNAS*, 109 (44), 17758–17764, 2012**

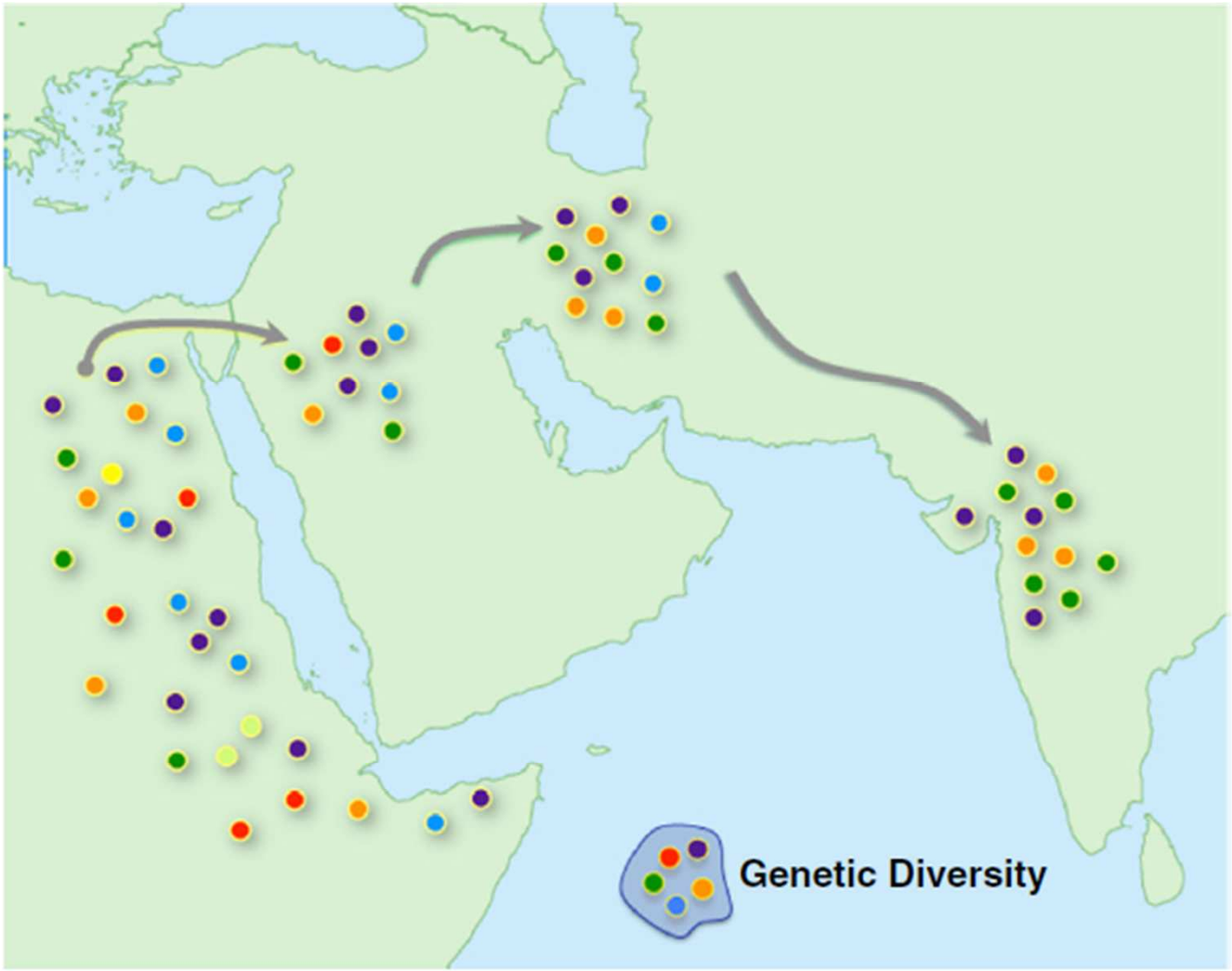


Fig. 2. Schematic of a serial found effect. We illustrate the effect of serial founder events on genetic diversity in the context of the OOA expansion. Colored dots indicate genetic diversity. Each new group outside of Africa represents a sampling of the genetic diversity present in its founder population. The ancestral population in Africa was sufficiently large to build up and retain substantial genetic diversity.

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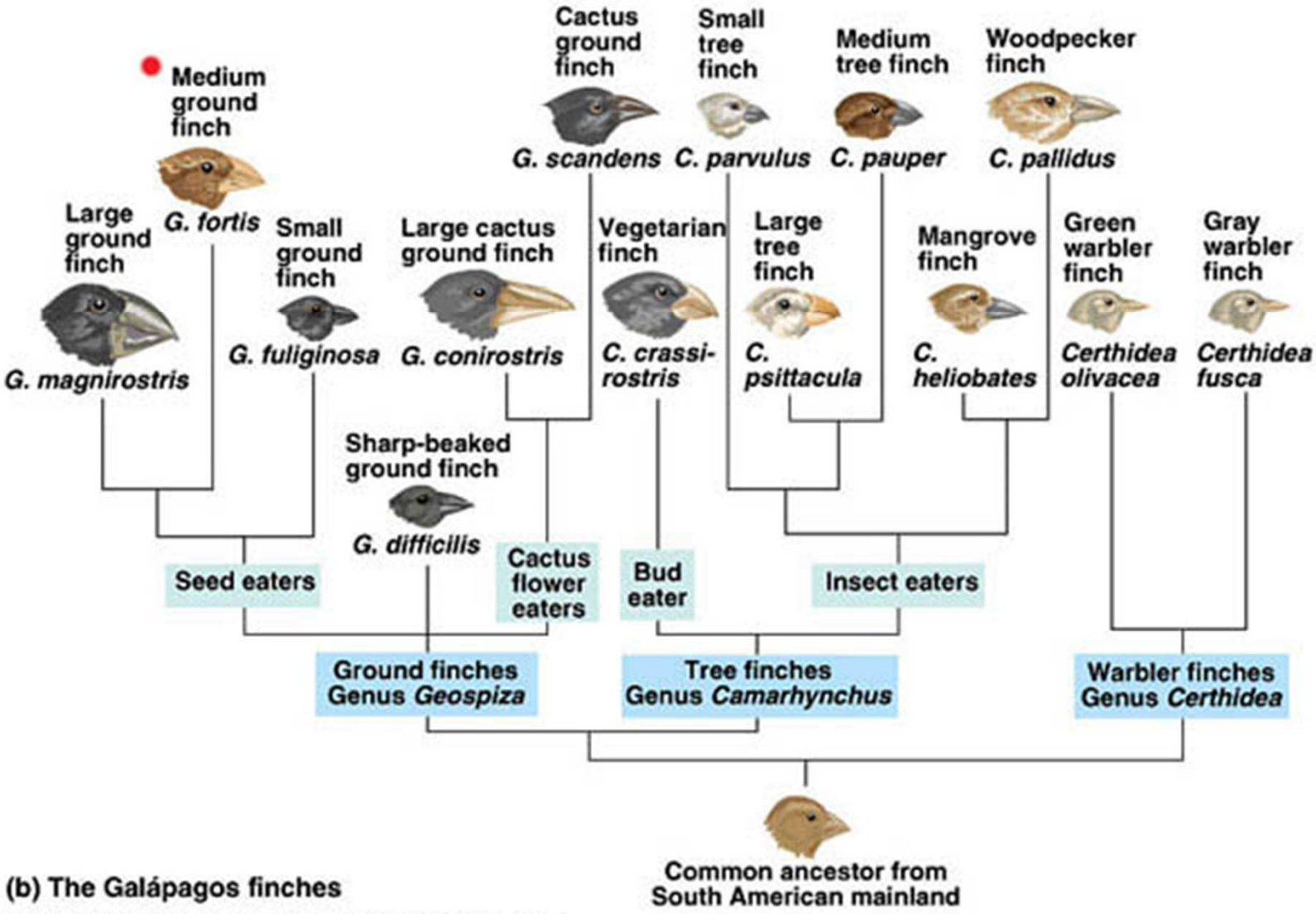


Which factors/causes for this adaptive radiation?

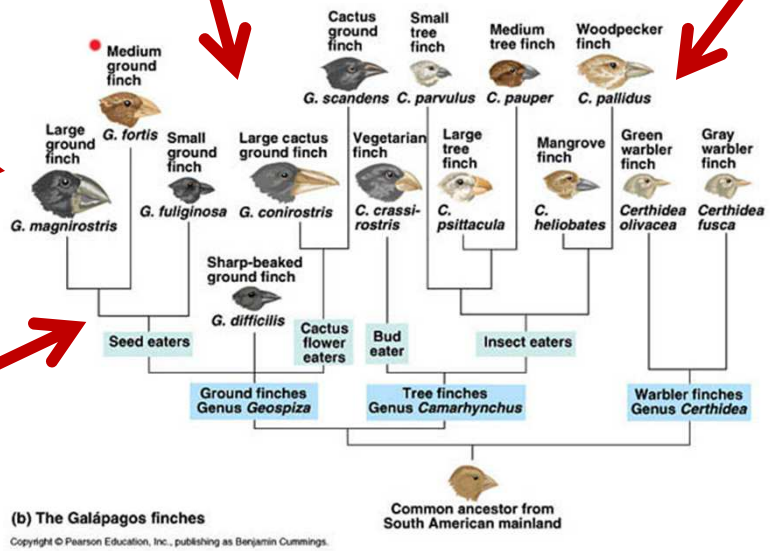
Natural and sexual selection

Random genetic drift

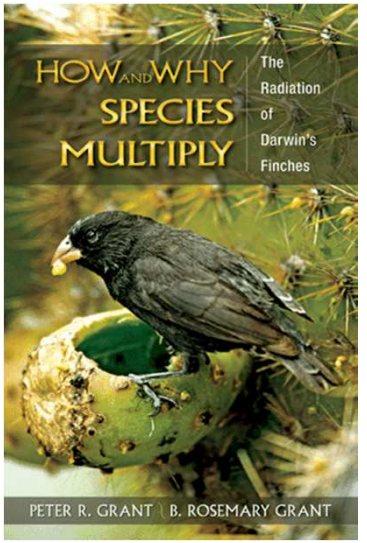
Cultural as well as genetic evolution

Hybridization

Fluctuations in climatic conditions



«In this book we attempt to explain the evolutionary diversification of Darwin's finches in terms of geography, behavior, ecology, and genetics. The explanation involves **natural and sexual selection, random genetic drift, exchange of genes through hybridization (introgression), and cultural as well as genetic evolution.** Linking all these factors together is the **frequent and strong fluctuation in climatic conditions**» (R. and P. Grant, 2008, p. 11)



It is quite impossible to find the exclusive cause of a particular phenomenon in biology. Biology is the science of multiple causes, plus the probabilistic feature of the chain of events.

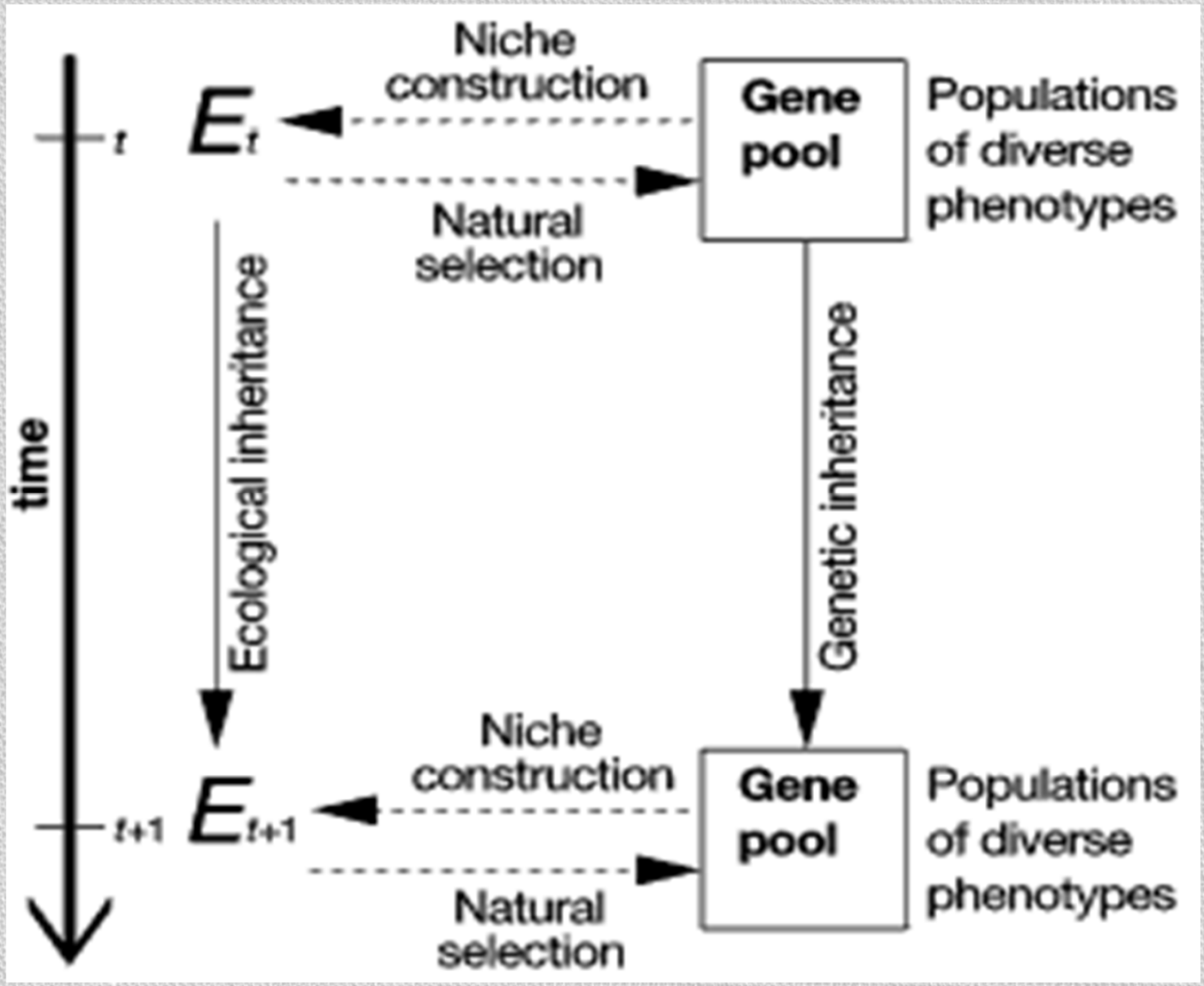
(Ernst Mayr, 1997)

PROXIMATE CAUSES (immediate physiological and mechanical factors; how eye works)

+

REMOTE CAUSES (evolutionary forces acting on traits; how eye evolved)

RECIPROCAL CAUSATION
(Niche construction)



COUNTERFACTUAL RESISTANCE

1. MAXIMUM – Deterministic process (no counterfactual possible)

2. MINIMUM – Random process (every counterfactual equi-probable)

3. MODULATION OF PROBABILITY – Evolutionary contingency (counterfactual probability depending on interplay between patterns and historical events)

EVOLUTIONARY CONTINGENCY

1) CONTINGENCY DOES NOT MEAN «PLAIN CHANCE»: IT IS AN **INTERPLAY BETWEEN REGULARITIES (PATTERNS) AND RANDOM EVENTS.**

2) CONTINGENCY IS A **MODULATION OF PROBABILITY** (DEPENDING ON THE RELATIVE POWER OF PATTERNS CASE BY CASE).

3) CONTINGENCY IS THE **CAUSAL POWER OF SINGLE EVENTS TO MODIFY HISTORICAL PATHS**: IT DEPENDS ON MULTIPLE INTERACTING CAUSES.

"We may define a cause to be **an object followed by another, and where all the objects, similar to the first, are followed by objects similar to the second**. Or, in other words, where, **if the first object had not been, the second never had existed.**" (DAVID HUME, 1748)

Regulatory definition of causality

Counterfactual definition of causality

CAUSES AND NARRATIVES…

Larry Gonick, "Cartoon History of the Universe"