The Evidence for Evolution — and the Thread of Homology

Source: The Princeton Guide to Evolution (Losos, ed., 2017)

Learning Objectives

PGE I.1–II.6

- Explain why the case for evolution rests on consilience, not one decisive experiment.
- Separate pattern (that change happened) from process (the mechanism) — and see why history accepted the first long before the second.
- Consider morphological and molecular evidence, and say what each independently demonstrates.
- Define homology and apply Patterson's three tests to classify any resemblance — structural or molecular.

Framing: Pattern vs. Process

PGE I.1

- Evolution = descent with modification — the pattern.
  - Within-species change AND the origin of new species.
- Natural selection = one process that can cause it — drift, mutation, and migration are others.
- Two pillars of evolutionary knowledge:
  - (1) the historical record of change (fossils, inferred phylogeny);
  - (2) the study of process (especially selection).
- Today is almost entirely pillar 1 — the evidence that descent happened.
    - Hinge concept: selection drives evolution only when the variation is heritable.

PART 1

A Brief History of Evolutionary Thought

Before Darwin: Setting the Stage

- **— a static 'ladder of nature'; no movement up or down.** Scala naturae
- **— the pre-1860 term for descent with modification.** Transmutation
- Geology supplies deep time and a tempo:
  - Uniformitarianism (Hutton, Lyell) — slow everyday forces over vast time → Darwin's gradualist template.
  - vs. Catastrophism — surface shaped by past large-scale catastrophes.
- Lamarck: inheritance of acquired characters — a heredity mechanism later rejected.

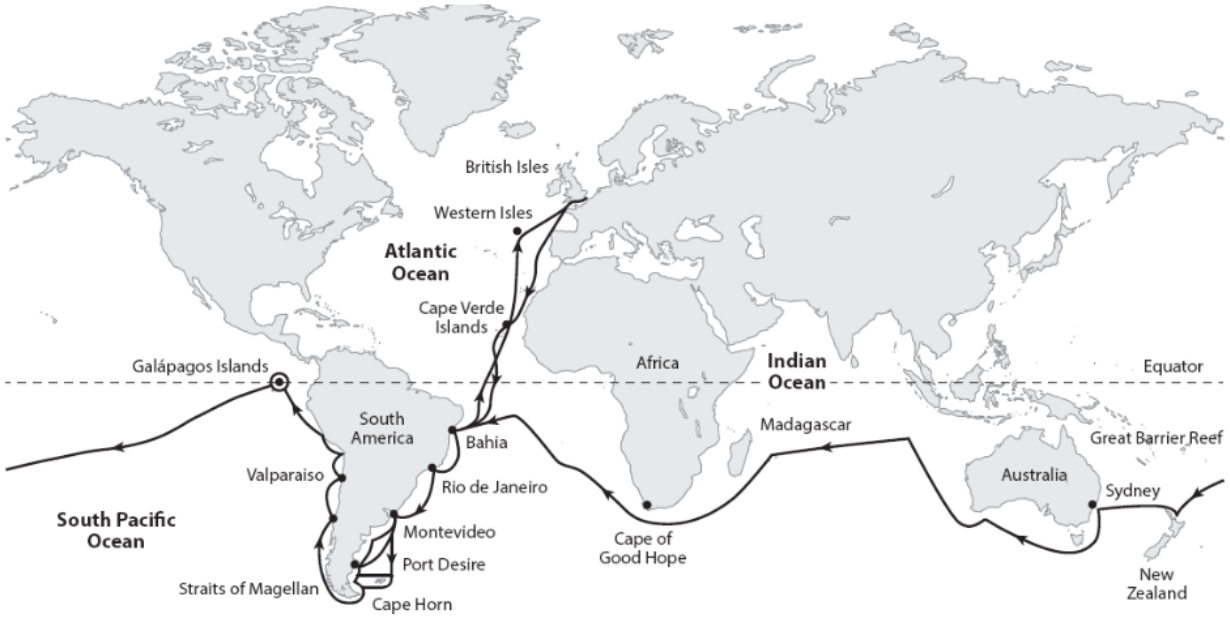


Figure 2. Path of the *Beagle* voyage between December 1831 and October 1836. The voyage completed an extensive around-the-world voyage, exposing Darwin to environments as different as the Canary Islands, the east and west coasts of South America, the Galápagos archipelago, the South Seas, and Australia. (From Jeffrey J. W. Baker and Garland E. Allen. 1982. *The Study of Biology*. Reading, MA: Addison-Wesley, 676; used with permission of the authors.)

Darwin as a Composite Paradigm — Mayr's Five Theories

- The Origin is not one idea but five separable claims:
  - 1. Evolution as such (descent with modification)
  - 2. Common descent
  - 3. Gradualism
  - 4. Multiplication of species
  - 5. Natural selection
- Why it matters: a critic who 'rejects Darwinism' usually rejects only one of these — diagnose which.

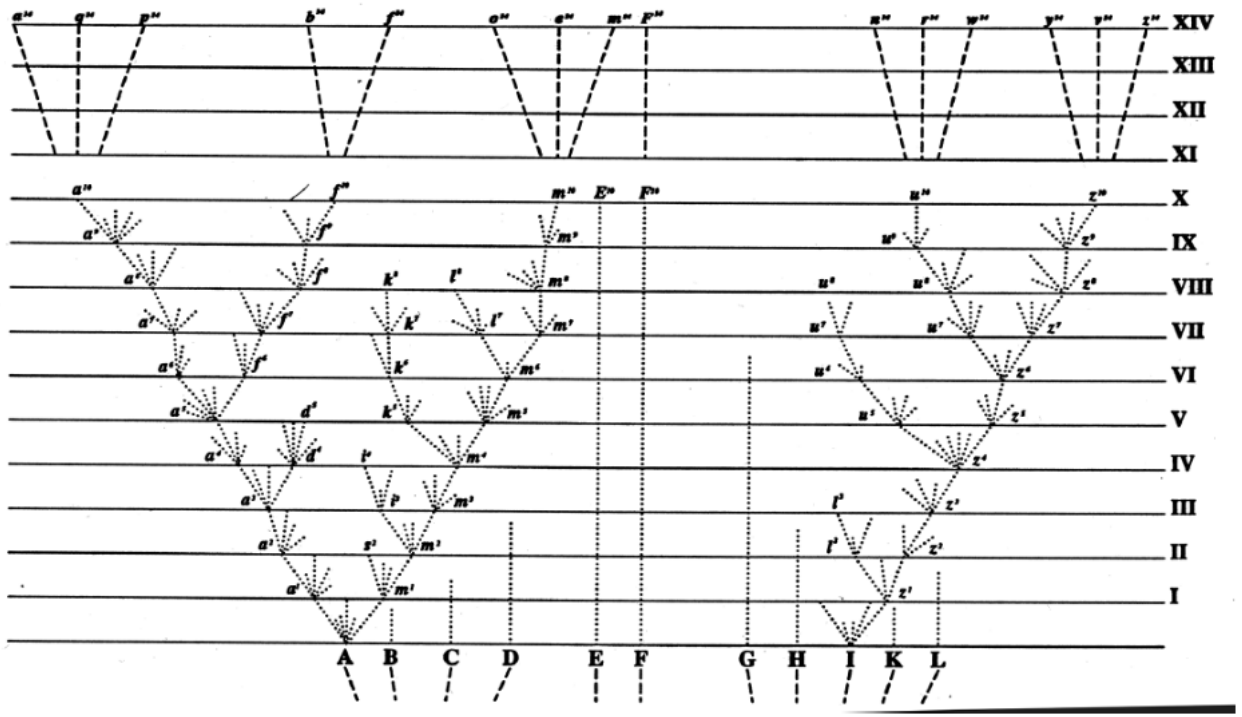


Figure 3. Darwin's diagram in *The Origin*, showing divergence from common ancestors. Horizontal lines represent time periods, from most remote (I) to most recent (XIV). Darwin was aware that most lineages go extinct, as evidenced by the lines that end at a certain point in time. (From Charles Darwin. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Existence*. London: John Murray.)

The Irony: Descent Won Early, Selection Nearly Died

- By the 1870s common descent was broadly accepted.
- By 1900 natural selection was nearly 'dead' — the 'eclipse of Darwinism':
  - neo-Lamarckism, orthogenesis (e.g., Irish elk antlers), mutationism.
- So the evidence for the pattern was already overwhelming — the fight was about the mechanism.

Why Selection Stalled: The Heredity Problem

- Blending inheritance diluted favorable variants each generation — a fatal flaw.
- The source of variation was unknown.
- The Mendelian–biometrician dispute (1901–1908):
  - Biometricians (Galton, Pearson) defended Darwin's continuous variation + statistics.
  - Mendelians (Bateson) championed discrete factors; each side dismissed the other.
- Rediscovering Mendel (1900) did NOT instantly rescue Darwinism.

The Modern Synthesis Resolves It (~1918–1960)

PGE I.2

- Fisher, Wright, Haldane: discrete Mendelian genes change frequency under weak selection.
  - Evolution redefined as change in gene frequency over time.
- Population thinking (Mayr) replaces typological thinking — variation is the raw material, not the 'type'.
- Wright adds genetic drift and the shifting-balance theory.
- Continuous variation and particulate inheritance are finally reconciled → population genetics.

PART 2

The Evidence — Consilience of Inductions

Darwin's One Idea Explains Three Patterns at Once

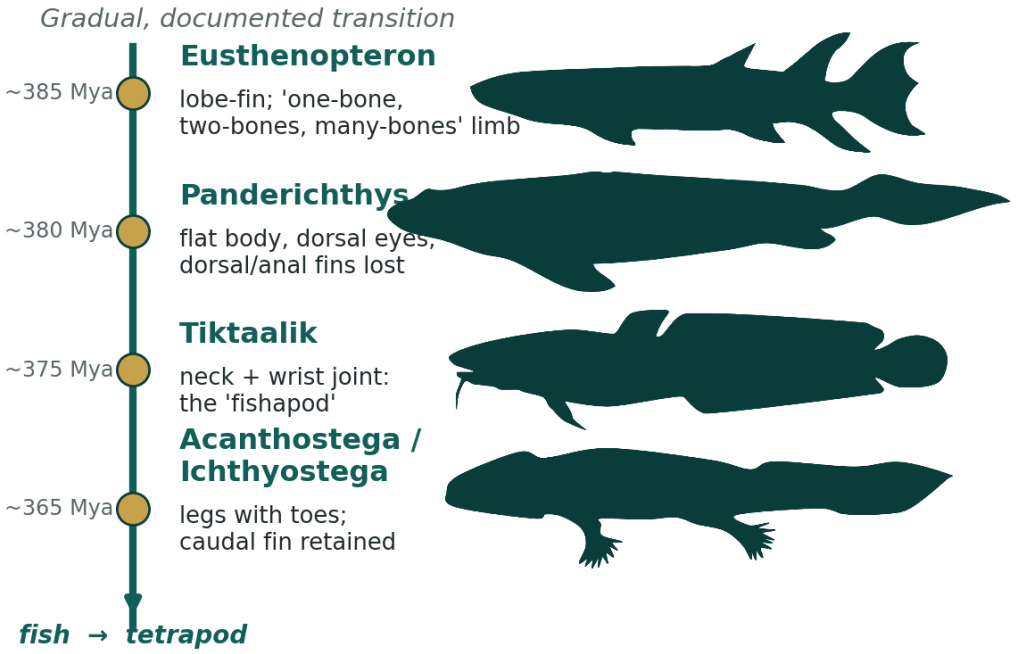
PGE I.3

Pattern	What it is	Darwin's explanation
Progression	earlier fossil forms succeeded by more diversified later ones	history over geological time
Unity of type	structural similarity exceeding any functional need	inheritance from common ancestors (= homology)
Adaptation	features fitting organisms to their conditions	modification of that inheritance by selection

Consilience (Whewell): independent lines converging on one explanation — the strength is in the convergence, not any single proof.

Transitional Fossils: The Fish → Tetrapod Walk

- A graded series — not a single 'missing link'.
- Each form adds a feature: limb pattern → flat body → neck + wrist → toes.
- Where 'fish' ends and 'tetrapod' begins is a matter of convention.
  - Exactly the continuity that descent predicts.



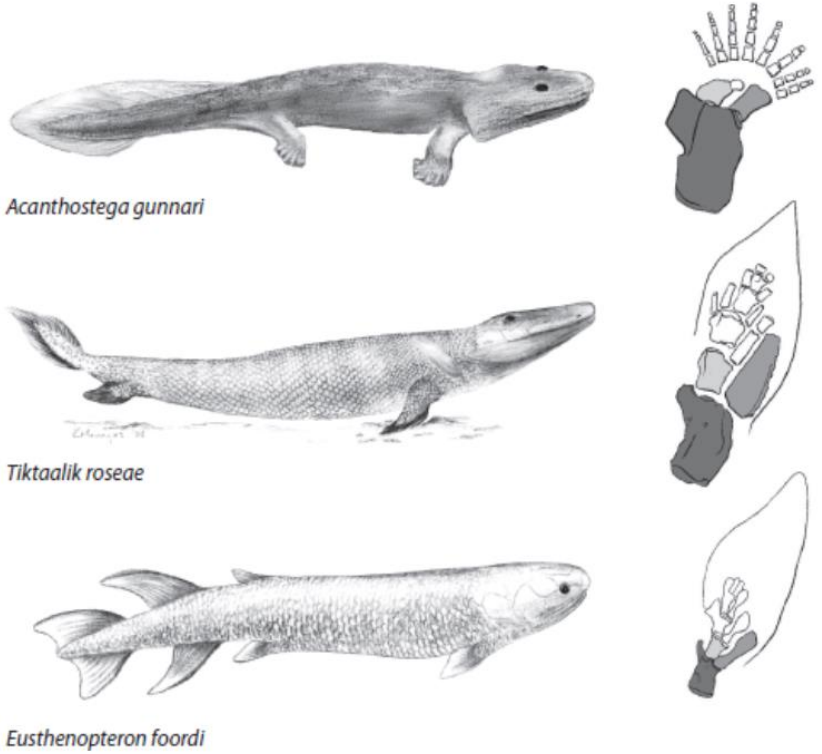
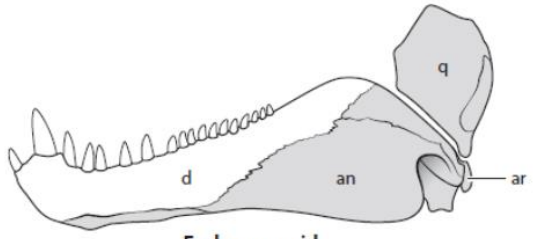


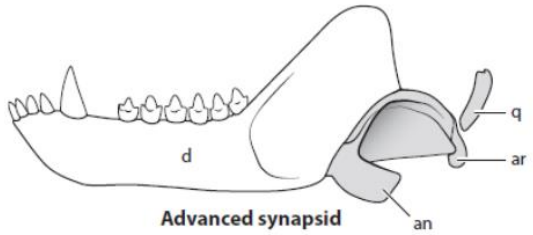
Figure 3. Transition from lobe-finned fish to tetrapods. The lobe-finned osteolepiform fish *Eusthenopteron* has the tetrapod-like "one bone, two bones, many bones" pattern in its fin. *Tiktaalik*, the "fish-apod," has lost the dorsal and anal fins, the head is free of the shoulder girdle, the snout is elongated with the eyes directed upward, and there is a wrist joint in the forelimb. *Acanthostega*, one of the first tetrapods, has digits but retains the caudal fin of its fish ancestors. The bones of the left forelimb shown in gray are, from darkest to lightest, the humerus, the radius, and the ulna, respectively; more distal elements are unshaded. (Copyright Kalliopi Monoyios.)

More Transitionals — and the 'Gaps' Misconception

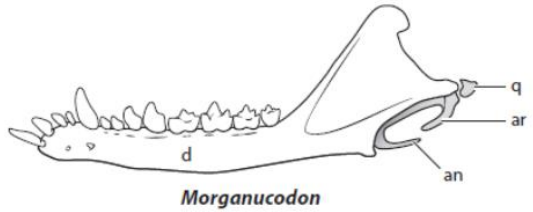
- Archaeopteryx (reptile–bird); the synapsid jaw-bone → mammalian ear-ossicle series.
- Misconception: 'gaps in the record disprove evolution.'
  - The record is admittedly imperfect (<1% of species fossilized)…
  - …yet predicted transitional forms keep being found where theory says to look.
- Prediction + discovery is stronger evidence than a complete-but-unpredicted record would be.



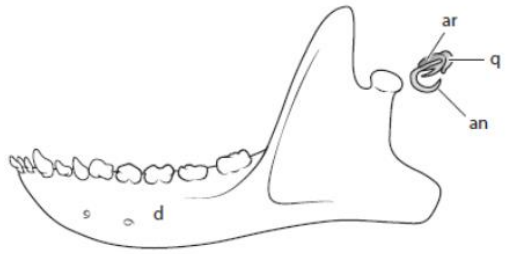
Early synapsid



Advanced synapsid



Morganucodon



Advanced mammal

Vestiges & Homologous Structures

- Vestiges: reduced/repurposed structures that betray 'tinkering' with an inherited body plan.
- Homologous structures: the same bones, different jobs — tetrapod forelimb as arm, wing, flipper, paddle.
  - Similarity exceeds any functional requirement → inheritance, not design for the task.
- Unity of type IS homology.

Figure 5. External hindlimb of a snake, the ball python (*Python regius*). Located just lateral to the anal scale, the keratinous claw is here shown slightly pushed away from the body by a probe. The claw is underlain internally by rudiments of the femur and, deeper in the body, the pelvis. (Photo by G. C. Mayer.)

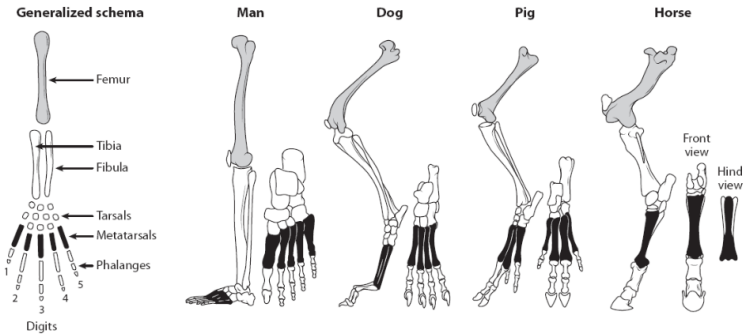


Figure 1. Comparison of the hind appendages of four vertebrates, showing the homologous relationships among the bones. All the femurs are homologous to each other, as are the tibia, fibula, and tarsals; metatarsals; and phalanges. It is evident the same bones have been modified for quite different functions over time. Such comparative homologies provided strong evidence for evolution, as descent with modification from a common ancestor. Special creationists would have to argue that the Creator repeatedly used the same archetypal form, as in the generalized appendage on the far left, for all vertebrate appendages. (From Jeffrey J. W. Baker and Garland E. Allen. 1982. *The Study of Biology*. Reading, MA: Addison-Wesley, 671; used with permission of the authors.)

Biogeography: The Reachability Rule

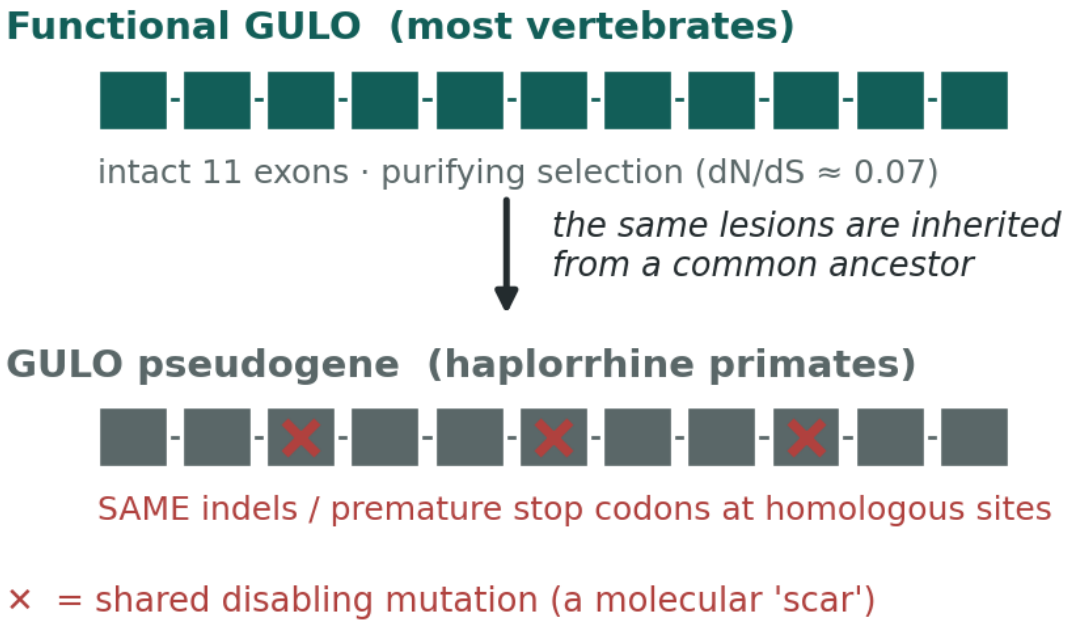
- Related species occur in connected areas, or areas a common ancestor could reach.
- Oceanic islands (e.g., Bermuda): filtered faunas of good water-crossers only.
- Marsupial Australia; Gondwanan distributions (e.g., Cynognathus across now-separated continents).
- Distributions reflect history (distance, barriers, drift, dispersal) — not habitat suitability alone.

Figure 8. Endemic and invasive oceanic island species. Left: The endemic Bermuda skink (*Eumeces* [*Plestiodon*] *longirostris*) is the only extant native terrestrial reptile of Bermuda. Its nearest relatives are from the nearest mainland, North America, 1000 km to the west. Right: A Bermudian specimen of *Bufo* (*Rhinella*) *marinus*, native to Middle and South America, and introduced to Bermuda in 1885. It is one of several exotic amphibian and reptile species that have thrived and even become pests there, after the barrier to dispersal was overcome by human agency. (Skink photo by Richard Ground; toad photo by G. C. Mayer.)

Molecular Evidence I — Shared Pseudogenes (GULO)

Yang 2013

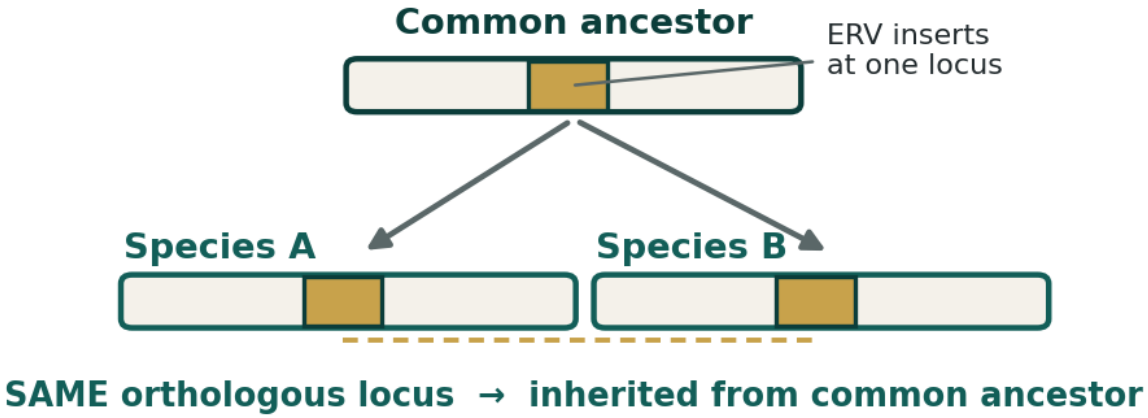
- GULO makes the last step of vitamin-C synthesis — a pseudogene in haplorrhine primates.
- Primates share the SAME inactivating lesions at homologous sites.
  - Inherited from a common ancestor, not lost independently.
- A shared molecular 'scar' — the strongest molecular line here.



Molecular Evidence II — ERVs at Orthologous Loci

Johnson 1999/2019

- ERVs: inherited remnants of ancient germline infections (~8% of our genome).
- A provirus at the SAME orthologous locus = inherited from a common ancestor.
  - Independent integration at the identical site is astronomically unlikely.
- Caveat: only shared orthologous insertions count (cf. PTERV1).



Caveat — only shared ORTHOLOGOUS insertions count

PTERV1: ~96% of insertions at NON-orthologous sites, absent in humans → independent integrations, not a shared-ancestry marker.

Molecular Evidence III — Amino Acid Differences Tracks Phylogeny

Ayala 1986

- Amino-acid differences scale with divergence time.
- Molecular homology recovers the SAME nested tree as morphology.
- Honest caveat: approximately, not strictly, clocklike.
  - Rates vary among lineages; deep times saturate (Ayala 1986).

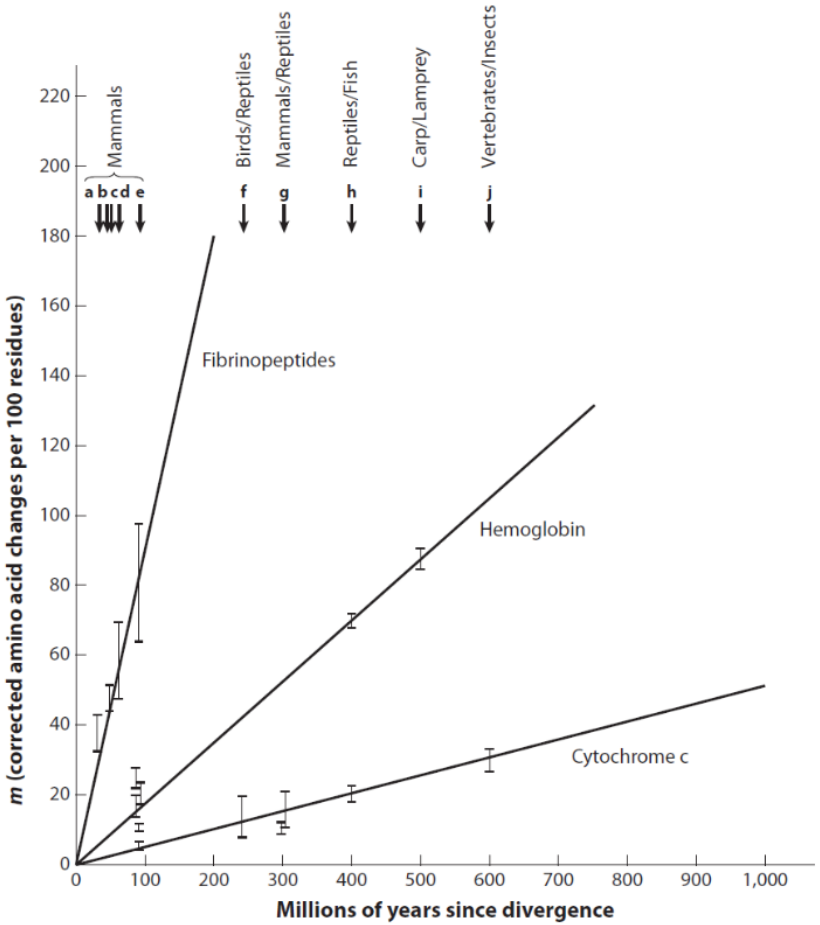


Figure 1. Molecular clocks. Rates of amino acid substitution in three proteins: fibrinopeptides, hemoglobin, and cytochrome *c*. The number of amino acid differences (per 100 residues, and corrected for multiple changes at the same residue) is plotted for comparisons between various mammals, birds and reptiles, mammals and reptiles, reptiles and fish, carp and lamprey, and vertebrates and insects, all lineages of organisms for which fossil data provided estimates of the time since divergence. Note that while some comparisons of the three proteins are fromthe same pair of organisms and time of divergence, the three proteins are

Molecular Evidence IV — A (Near-)Universal Code, Formally Tested

Theobald 2010

- A nearly universal genetic code + shared core machinery point to a single common ancestor.
- Theobald (2010): a formal model-selection test of universal common ancestry (UCA).
  - UCA overwhelmingly favored over independent-origin models — even allowing horizontal gene transfer.
  - Signal comes from nested phylogenetic structure, not mere sequence similarity (2011 rebuttal).
- The code is near-universal: lineage variants are derived modifications — descent with modification itself.

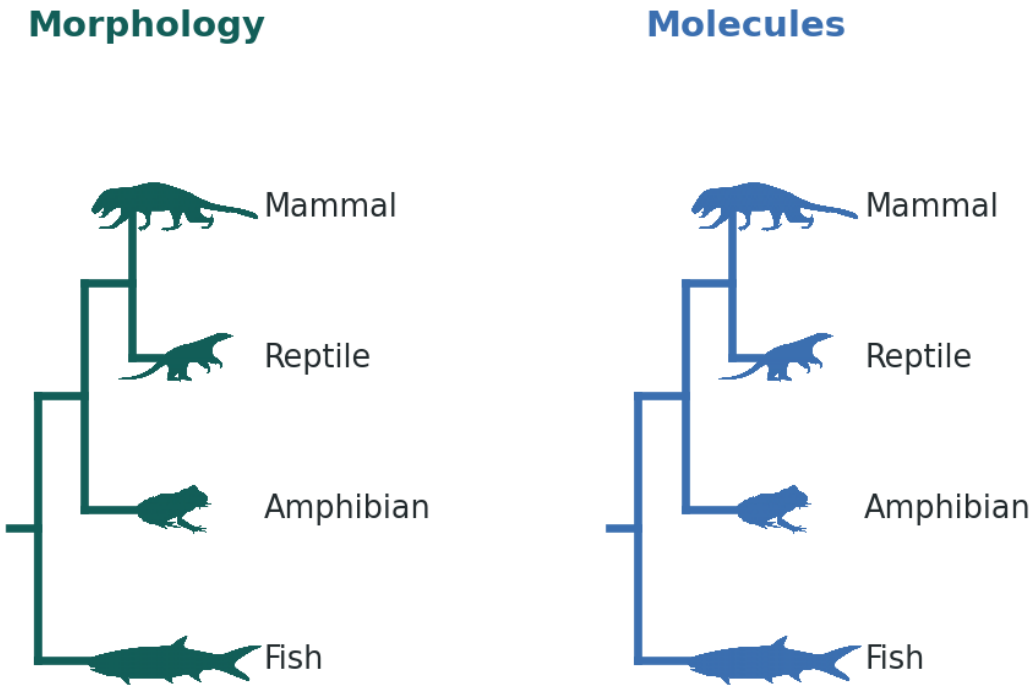
Codon	*Amino acid*	*Codon*	*Amino acid*	*Codon*	*Amino acid*	*Codon*	*Amino acid*
TTT	Phenylalanine (Phe)	TCT	Serine (Ser)	TAT	Tyrosine (Tyr)	TGT	Cysteine (Cys)
TTC		TCC		TAC		TGC	
TTA	Leucine (Leu)	TCA		TAA	Stop	TGA	Stop
TTG		TCG		TAG		TGG	Tryptophan (Trp)
CTT		CCT	Proline (Pro)	CAT	Histidine (His)	CGT	Arginine (Arg)
CTC		CCC		CAC		CGC	
CTA		CCA		CAA	Glutamine (Gln)	CGA	
CTG		CCG		CAG		CGG	
ATT	Isoleucine (Ile)	ACT	Threonine (Thr)	AAT	Asparagine (Asn)	AGT	Serine (Ser)
ATC		ACC		AAC		AGC	
ATA		ACA		AAA	Lysine (Lys)	AGA	Arginine (Arg)
ATG	Methionine (Met)	ACG		AAG		AGG	
GTT	Valine (Val)	GCT	Alanine (Ala)	GAT	Aspartic acid (Asp)	GGT	Glycine (Gly)
GTC		GCC		GAC		GGC	
GTA		GCA		GAA	Glutamic acid (Glu)	GGA	
GTG		GCG		GAG		GGG	

Figure 1. The genetic code

Bridge: Morphology + Molecules = One Argument

PGE I.3 / II.6

- Every line above is the SAME inference: nested similarity from shared ancestry.
- Bones and sequences recover the same nested tree.
- Independent data, independent methods, one congruent hierarchy → consilience.
- That hierarchy has a name — and a test. It is homology.



Independent data → the SAME nested tree (congruence)

Evolution in Action — Change We Can Watch

PGE I.1 / I.3

- Endler's Trinidad guppies: moved to predator-free streams, evolved bright male coloration in ~14 generations.
- Industrial melanism in Biston betularia; antibiotic and HIV drug resistance.
- Darwin's finches; polyploid speciation in *Spartina anglica*.
- A class of evidence Darwin lacked: selection in nature is often strong — testable in real time.

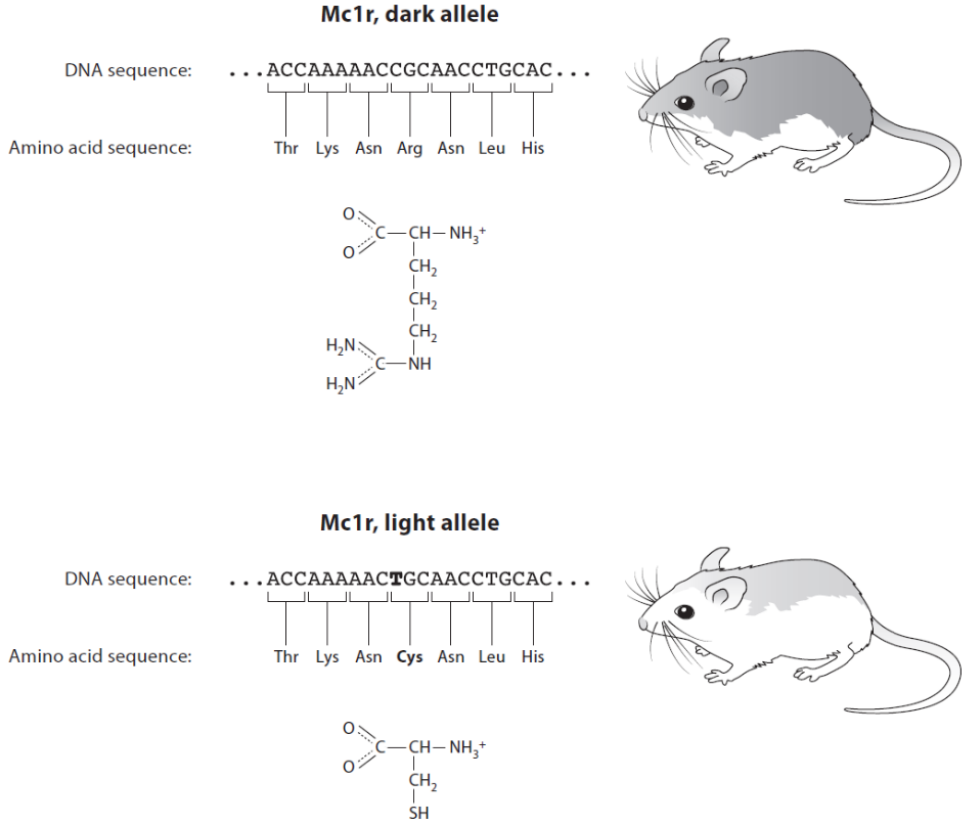


Figure 2. The coat coloration in beach mice is caused by one change (C to T) in the DNA sequence of *Mc1r*, which causes the codon CGC to turn into TGC, changing it from coding for arginine (Arg) into coding for cysteine (Cys). The chemical structures for Arg and Cys are shown; these two amino acids have very different chemical properties that translate into divergent functions of the protein, causing differences in the coat color of the mice. This is a nonsynonymous change, because the resulting protein sequence differs between the two alleles. In contrast, a change from CGC to CGA at that same codon, shown in the bottom

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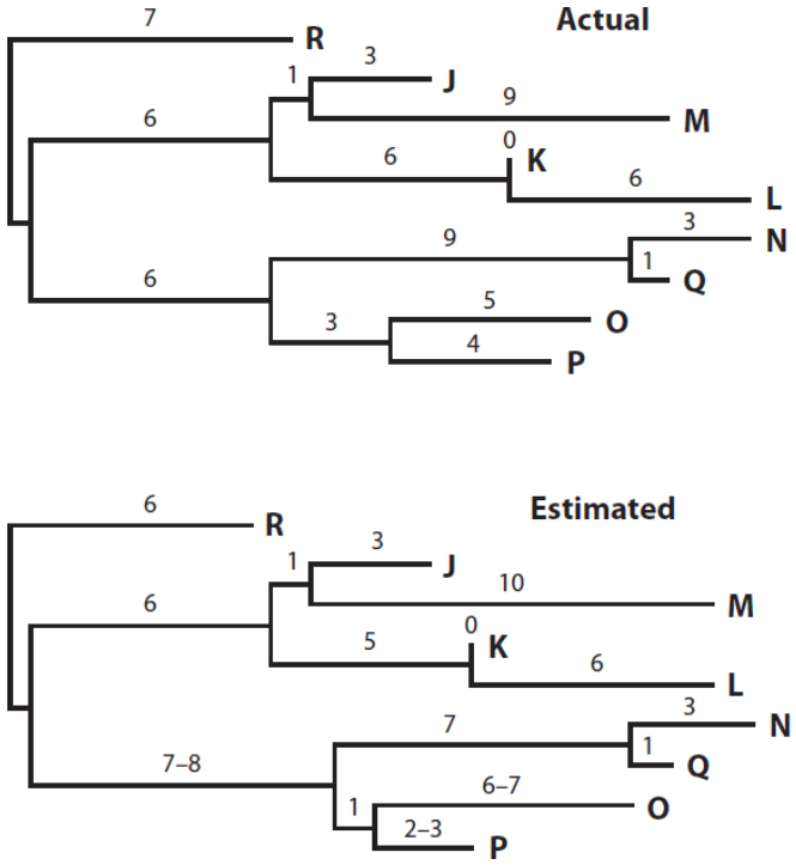


Figure 2. Mutational change in virus cultures demonstrates descent with modification and molecular evolution, and the molecular clock concept. Shown is a comparison of an actual "true" phylogeny of a virus (bacteriophage T7) with an estimated phylogeny constructed using only DNA sequences of the viruses in the experimental population. This population was initiated with one virus and split in binary fashion into several sequential derived lineages, the end points being denoted as the letters on the right side of the phylogeny. Numbers above the branches indicate the actual or estimated number of nucleotide substitutions that occurred along each branch, respectively. Actual substitutions were determined by sequencing 1091 base pairs of the ancestral viruses at each branch point in the tree. (Modified from David M. Hillis, John P. Huelsenbeck, and Clifford W.

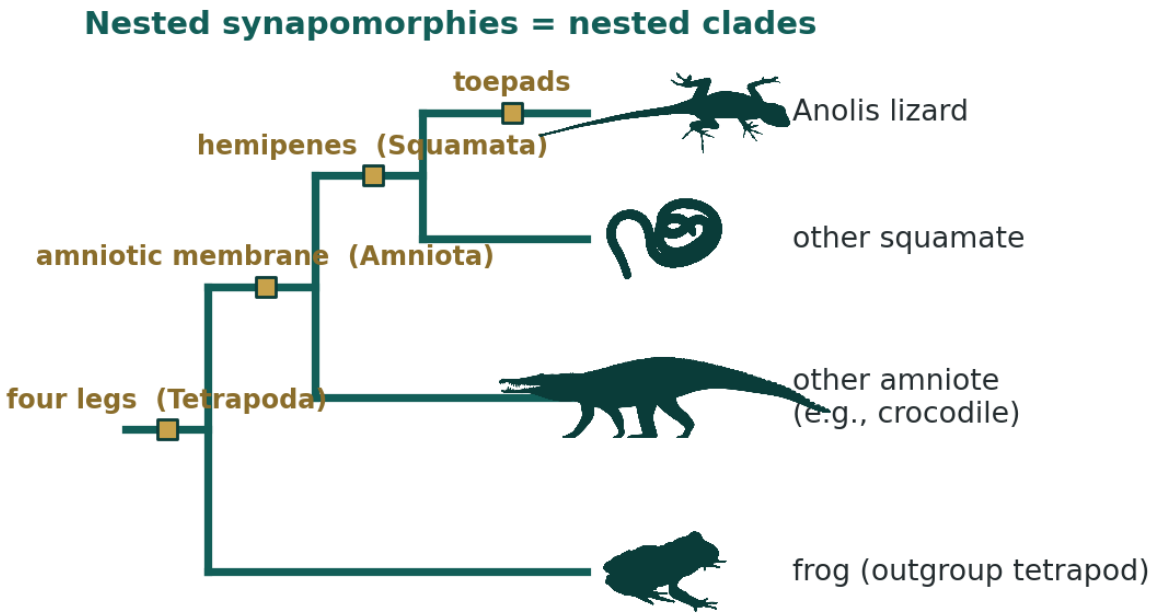
PART 3

The Thread of Homology

What Is Homology — and Why Nesting Is the Signature

PGE I.3 / II.6

- **Homology** — a character inherited from an equivalent character of a common ancestor.
- Homologies are NESTED: each derived trait marks a clade within a larger clade.
- Branching + inheritance only to descendants ⇒ nesting IS the signature of ancestry.



Each derived trait marks a clade nested within a larger one — the signature of common ancestry.

Resemblance ≠ Homology: Patterson's Three Tests

PGE II.6

Test	Question	A homolog must…
Similarity	structural / sequence correspondence?	pass (>70% DNA identity = definitive)
Conjunction	do both co-occur in one organism, one stage?	NOT co-occur
Congruence	do homologies form a nested hierarchy (cladogram)?	pass

Apply all three. The pattern of pass/fail classifies the resemblance (next slide).

The Pass/Fail Signature

PGE II.6

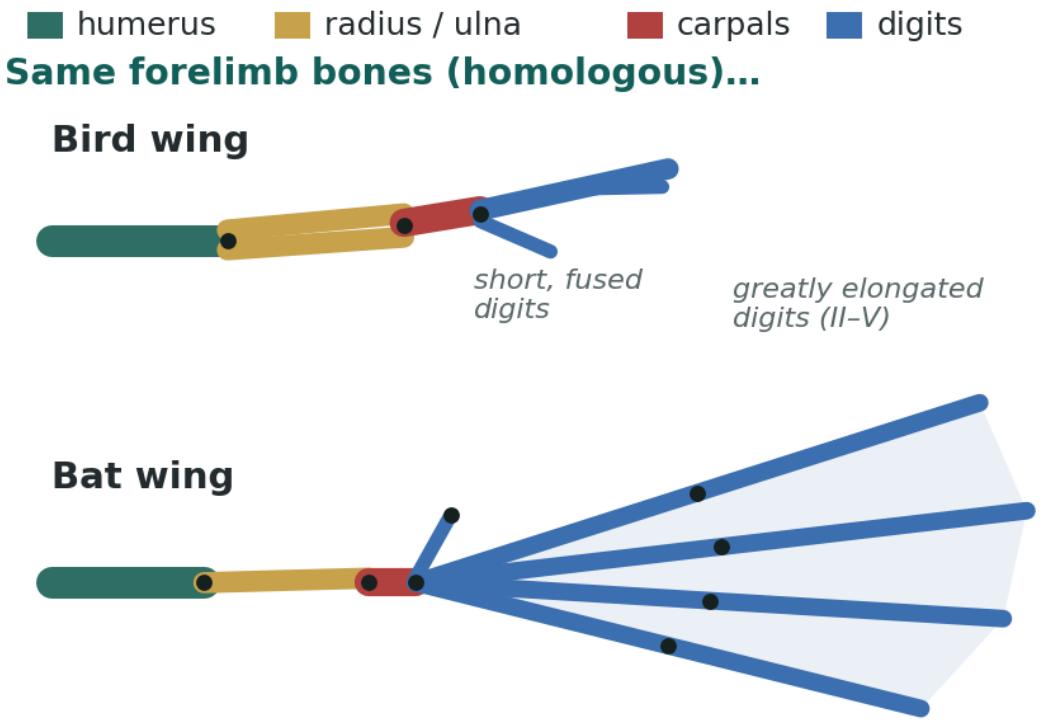
Resemblance	Similarity	Conjunction	Congruence
Homology	pass	pass	pass
Serial homology (paralogs)	pass	FAIL	—
Parallelism (deep homology)	pass	pass	FAIL
Convergence	FAIL	pass	FAIL

Serial homology = neck vs. trunk vertebrae, molecular paralogs. Parallelism = shared latent developmental pathway.

Worked Example: Are Bird and Bat 'Wings' Homologous?

PGE II.6

- Same forelimb bones (homologous); the WING is assembled differently.
- Similarity as 'wings' FAILS; conjunction passes; congruence FAILS.
  - 'wing' overlaps feathers (birds) vs hair/mammary glands (bats), non-nestedly.
- Resolution: split into two homologies → wings are CONVERGENT.
  - 'Wing' is a function, not a homology.



…built into different wings — the WING is convergent / analogous.

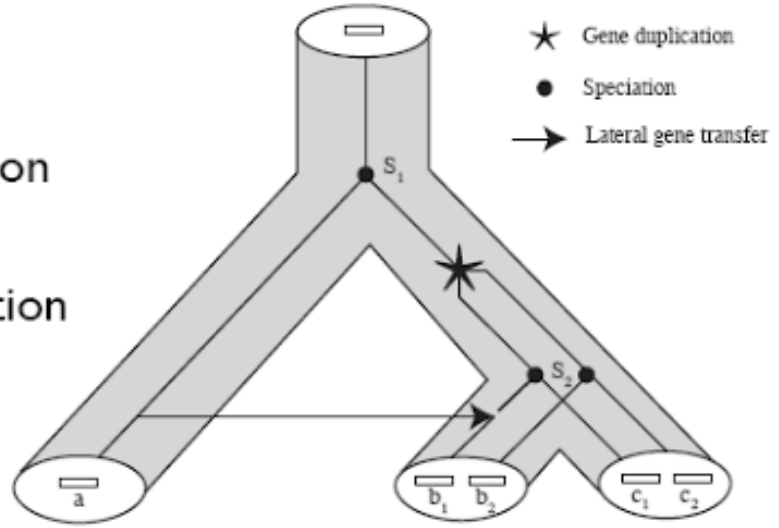
Molecular Homology: Orthology, Paralogy, Xenology

- The same three tests run on sequences — directly the logic of comparative genomics:
  - Conjunction separates orthologs from paralogs (duplicates co-occurring in one genome).
  - Congruence failure flags horizontal transfer (xenology) — a gene tree that won't reconcile with the species tree.
- Caution: gene-expression sharing ≠ structural homology.
  - Deep-homology modules build non-homologous structures; there is no one-to-one structure↔gene map.

Two genes (or characters) are *homologs* if they have a common ancestor.

Main Subtypes

- *Orthologs*: through speciation
- *Paralogs*: through duplication
- *Xenologs*: through lateral transfer



Synthesis & Key Takeaways

PGE I.1–II.6

- The case for evolution is consilience — independent lines converging, not one proof.
- History accepted the pattern (descent) long before the process (selection) — keep them distinct.
- Morphology and molecules recover the SAME nested tree; that hierarchy is homology.
- Homology is a hypothesis you TEST (Patterson's three tests), not a similarity you assume —
  - whether the character is a wrist bone or a gene.

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