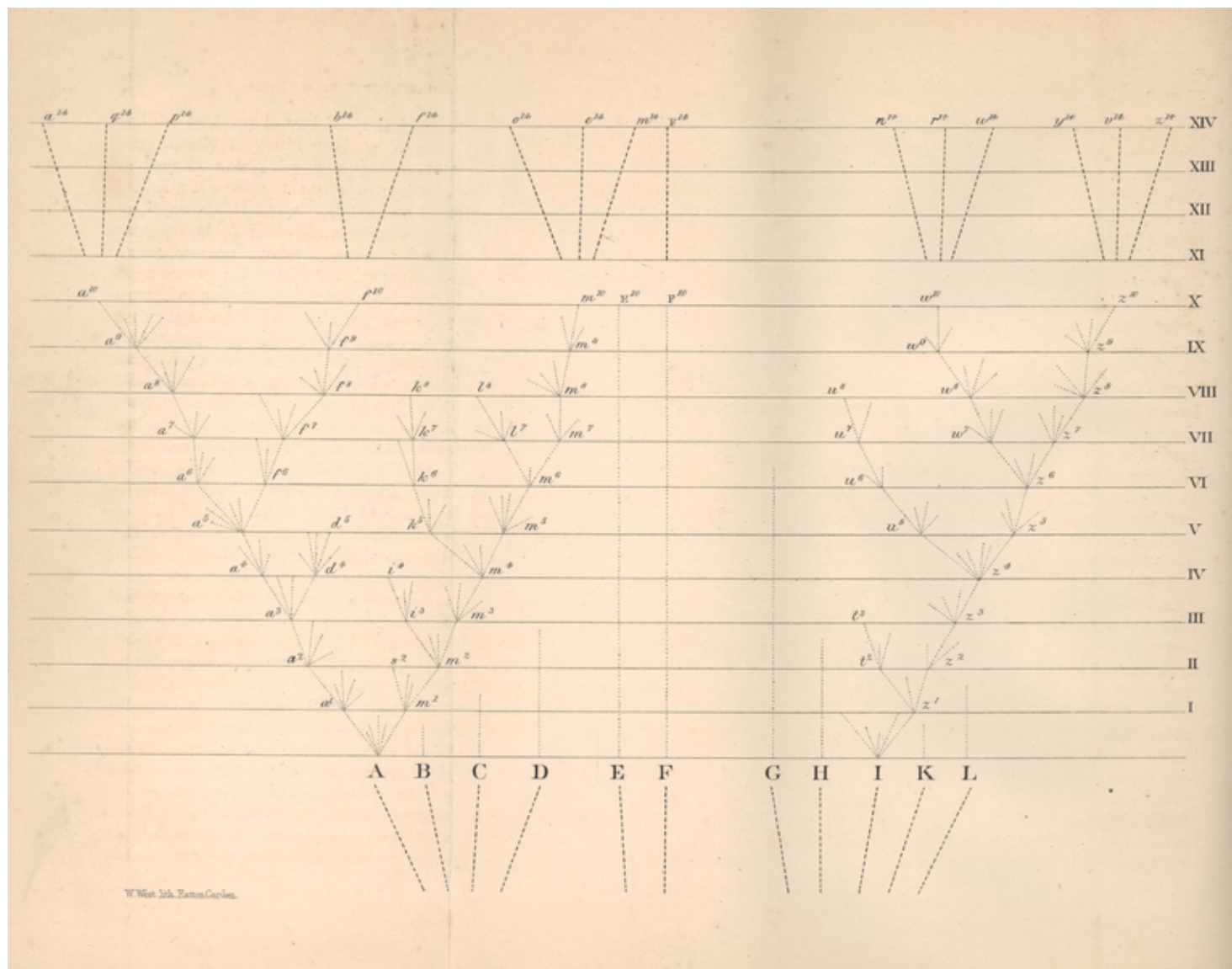


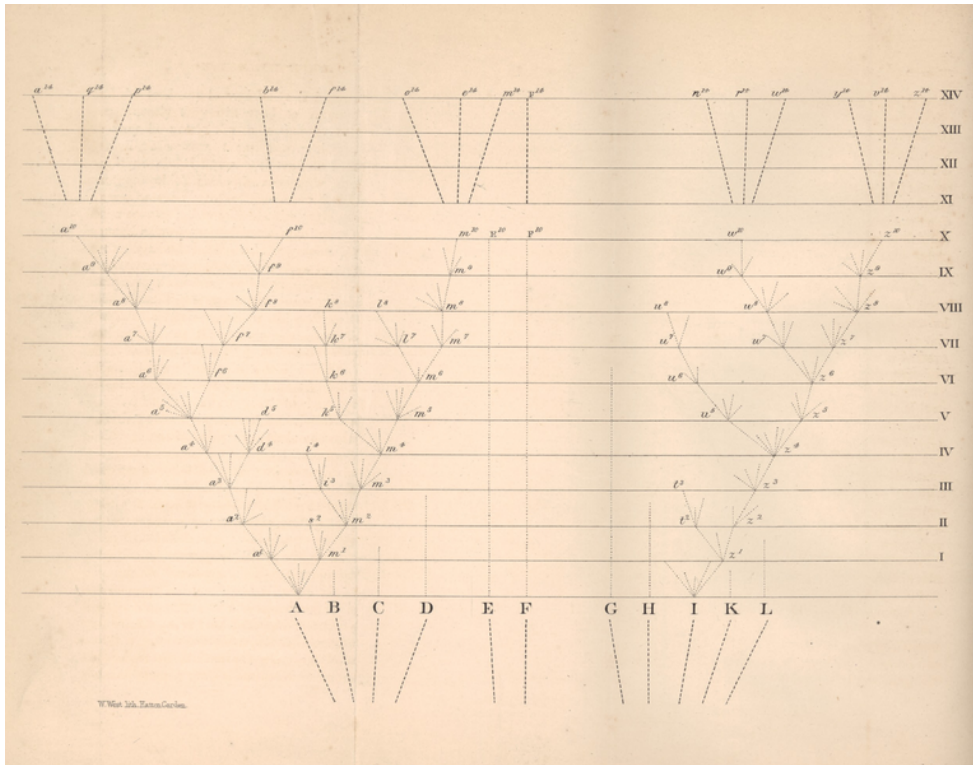
Evolutionary lineages and phylogenetics



(from: Darwin, C. 1859. *The Origin of Species*. John Murray, Albermarle St., London.)

Evolutionary lineages and phylogenetics

Darwin's observation formed the conceptual foundation for modern science of systematics



Developments in four main areas have had a profound impact on our ability to reconstruct the history of lineages

1) General acceptance and application of concepts (established by Willi Hennig in 1966)

2) Use of abundant characters within a DNA sequence

3) Continual improvements in our understanding of the tempo/mode of evolution of those characters

4) Using phylogeography to bridge the threshold between inter- and intraspecific boundaries

Evolutionary lineages and phylogenetics

Overview of this section:

- 1) Basic Phylogenetics
- 2) Phylogenetic reconstructions and vicariance
- 3) Phylogeography
- 4) Phylogenetic community structure

Goals and learning objectives

- 1) Be able to examine phylogenetic trees and describe relationships among groups (e.g., monophyletic groups, common ancestor, character state changes).**
- 2) Understand how phylogenetic reconstructions and vicariance underlie basic questions and goals in phylogeography**
- 3) Understand the terms that describe the phylogenetic structure of communities (e.g., patterns of clustering versus overdispersion in community phylogenetics)**

Phylogenetics

Reconstructing phylogenies (Important points to acknowledge):

1. There are different methods to reconstruct evolutionary relationships among taxa, each with various strengths, weaknesses, and assumptions.
2. Phylogenies are hypotheses – we cannot know the true pattern of ancestor-descendant relationships that make up a tree, we can only generate the *most probable, most likely, or most parsimonious* tree given the data at hand.
3. The field of *Phylogenetic Systematics*, and the associated philosophical principles and methods (developed by Willi Hennig in the 1960s) revolutionized the way in which people reconstructed phylogenies.
4. Robust phylogenetic reconstruction (i.e., adopting proper sampling of taxa and traits, and incorporating statistical assessments of the reliability of the resulting phylogenetic tree) is a key process in modern analytical biogeography.

Phylogenetics

Phylogenetic Systematics

Phylogenetic systematics: philosophy and methods for the reconstruction of ancestor-descendant (i.e. evolutionary) relationships among a set of taxa.

Basic tenets of phylogenetic systematics:

- 1) Characters used to reconstruct a phylogeny are modifications of existing characters. DNA sequence variation and morphological traits are the most commonly employed characters.
- 2) The history of changes in character states reflects the ancestor-descendant relationships of organisms bearing the characters.
- 3) The distribution of characters among a set of taxa is used to identify *monophyletic* groups. Monophyletic groups are also known as *clades* and phylogenetic trees are sometimes referred to as *cladograms*.
- 4) Monophyletic groups are identified by shared derived traits (also known as *synapomorphies*). All other taxa outside the monophyletic groups possess the ancestral or *plesiomorphic* traits.

Phylogenetics

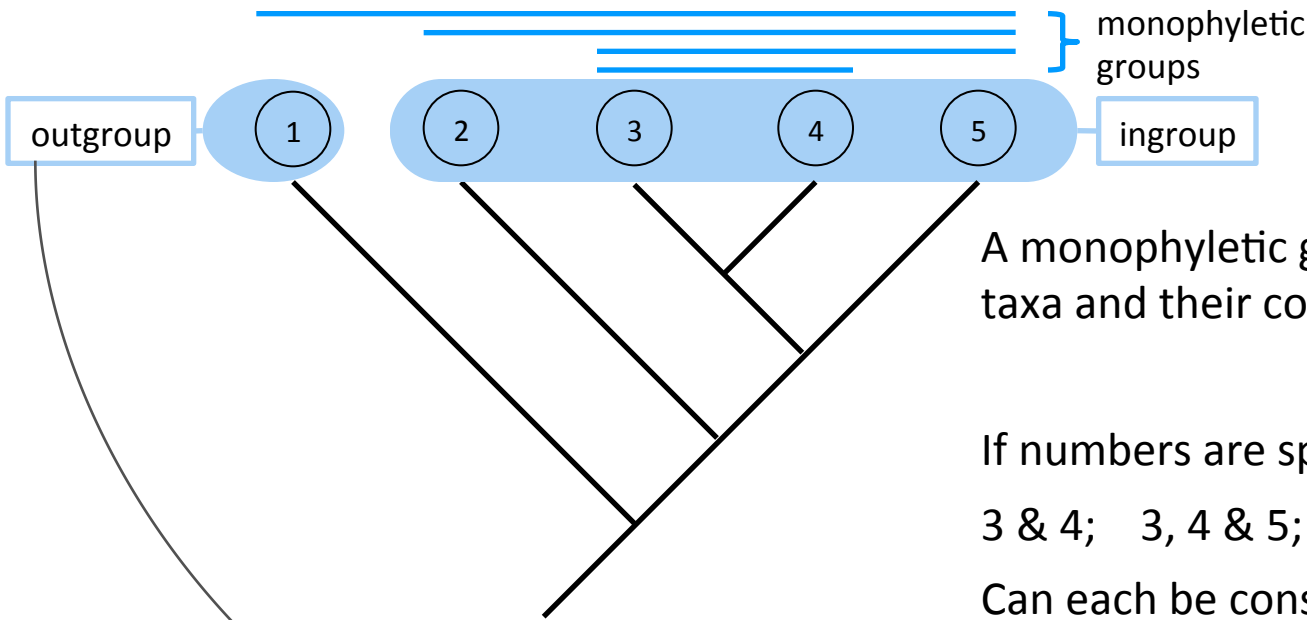
Phylogenetic Systematics Glossary:

- Monophyletic (clade):** a group of organisms which includes the most recent common ancestor of all of its members and all of the descendants of that most recent common ancestor
- Paraphyletic:** a group of organisms which includes the most recent common ancestor of all of its members, but not all of the descendants of that most recent common ancestor
- Polyphyletic:** a group of organisms which does not include the most recent common ancestor of those organisms; the ancestor does not possess the character shared by members of the group
- Homology:** two structures are considered homologous when they are inherited from a common ancestor which possessed the structure
- Plesiomorphy:** a primitive character state for the taxa under consideration
- Apomorphy:** a derived character state for the taxa under consideration
- Synapomorphy:** a character which is derived, and because it is shared by the taxa under consideration, is used to infer common ancestry
- Ingroup:** in cladistic analysis, the set of taxa which are hypothesized to be more closely related to each other than any are to the outgroup
- Outgroup:** in cladistic analysis, any taxon used to help resolve the polarity of characters, and which is hypothesized to be less closely related to each of the taxa under consideration than any are to each other
- Sister group:** the two clades resulting from the splitting of a single lineage

Phylogenetics

The Anatomy of Phylogenetic Systematics:

A natural taxon is defined as a monophyletic group (also called a clade)
this is a monophyletic branch in a phylogeny



A monophyletic group includes all descendant taxa and their common ancestor

If numbers are species...

3 & 4; 3, 4 & 5; 2, 3, 4 & 5; 1, 2, 3, 4 & 5

Can each be considered monophyletic groups

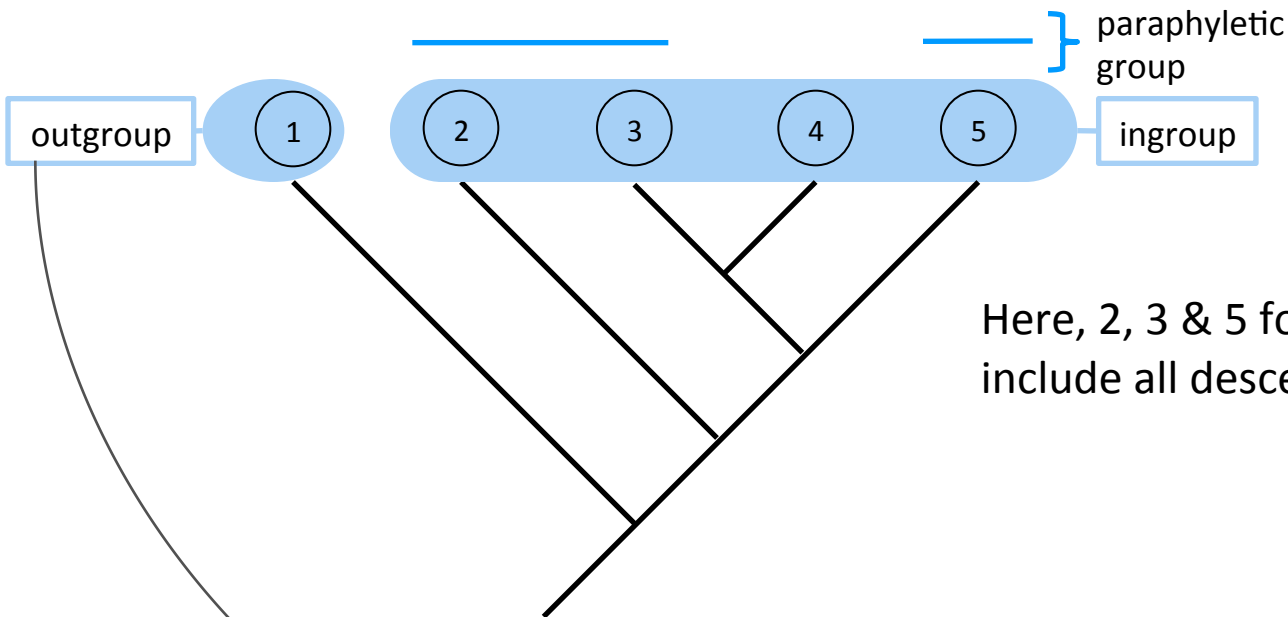
Outgroup allows identification of ancestral character states.

From Lomolino et al. 2010

Phylogenetics

The Anatomy of Phylogenetic Systematics:

A paraphyletic group includes the most recent common ancestor, but not all of its descendants



Here, 2, 3 & 5 form a group that does not include all descendants (missing 4)

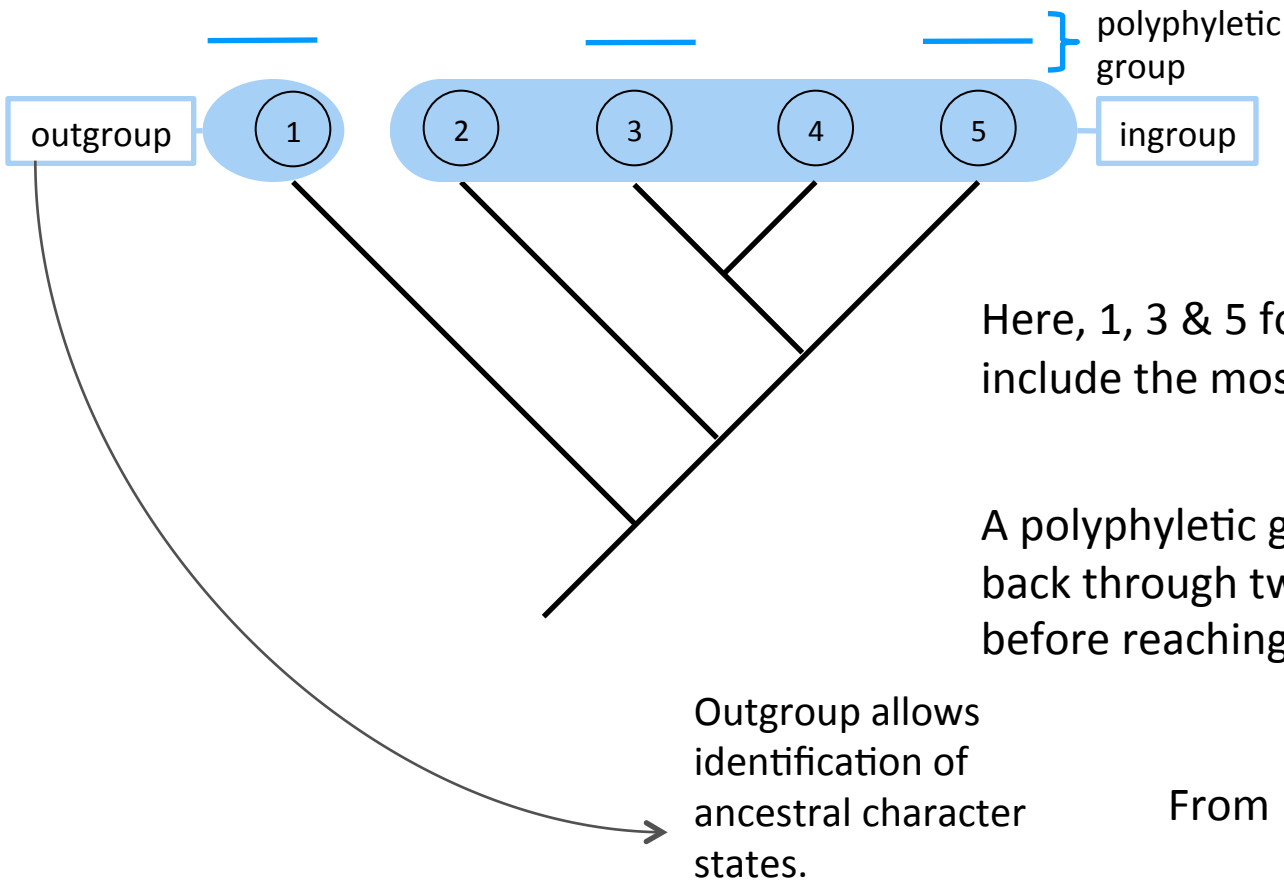
Outgroup allows identification of ancestral character states.

From Lomolino et al. 2010

Phylogenetics

The Anatomy of Phylogenetic Systematics:

A polyphyletic group is composed of a collection of organisms in which the most recent common ancestor is not included

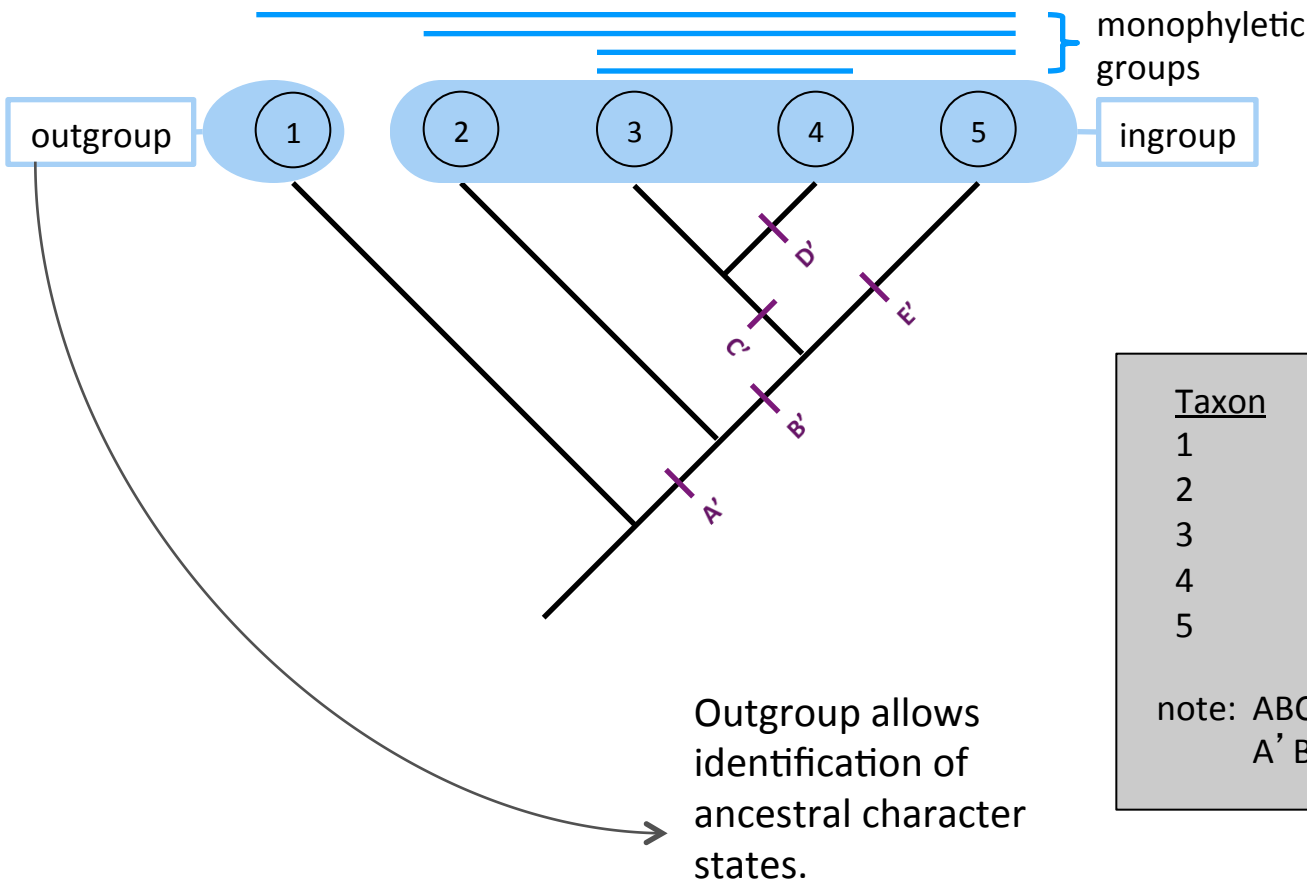


From Lomolino et al. 2010

Phylogenetics

Phylogenetic Systematics

A common criterion for inferring phylogenies is *maximum parsimony*: an optimality criterion that minimizes the total number of character state changes in the tree.



<u>Taxon</u>	<u>Character States</u>
1	A B C D E
2	A' B C D E
3	A' B' C' D E
4	A' B' C' D' E
5	A' B' C D E'

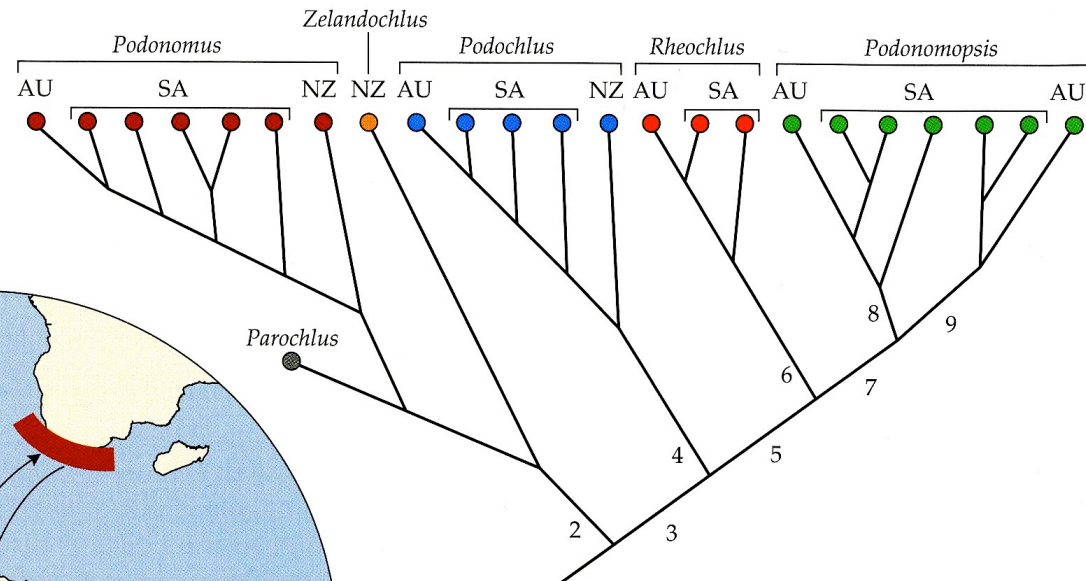
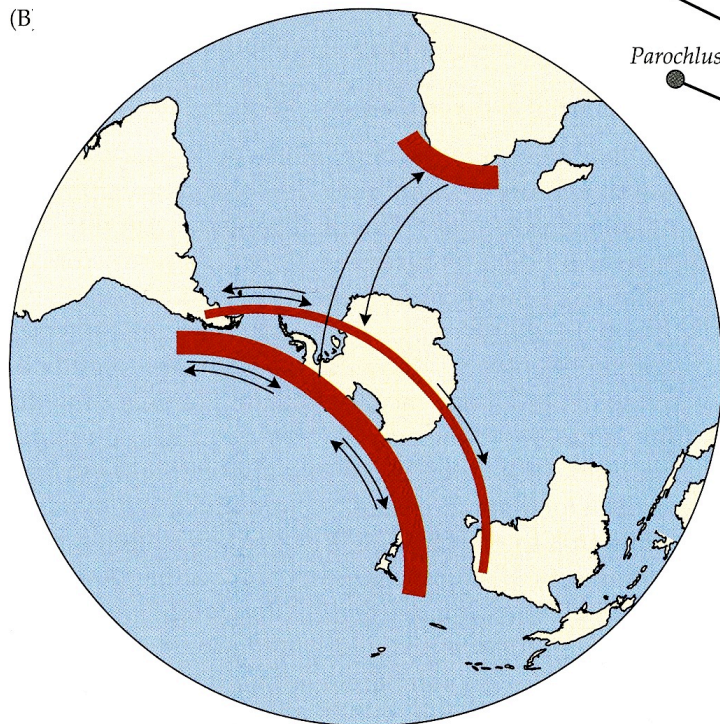
note: ABCDE are ancestral character states
A' B' C' D' E' are derived character states

Phylogenetic reconstructions

Lars Brundin, a Swedish entomologist, was among the first to conduct a phylogenetic reconstruction of the biogeographic history of a taxon (southern hemisphere midges)



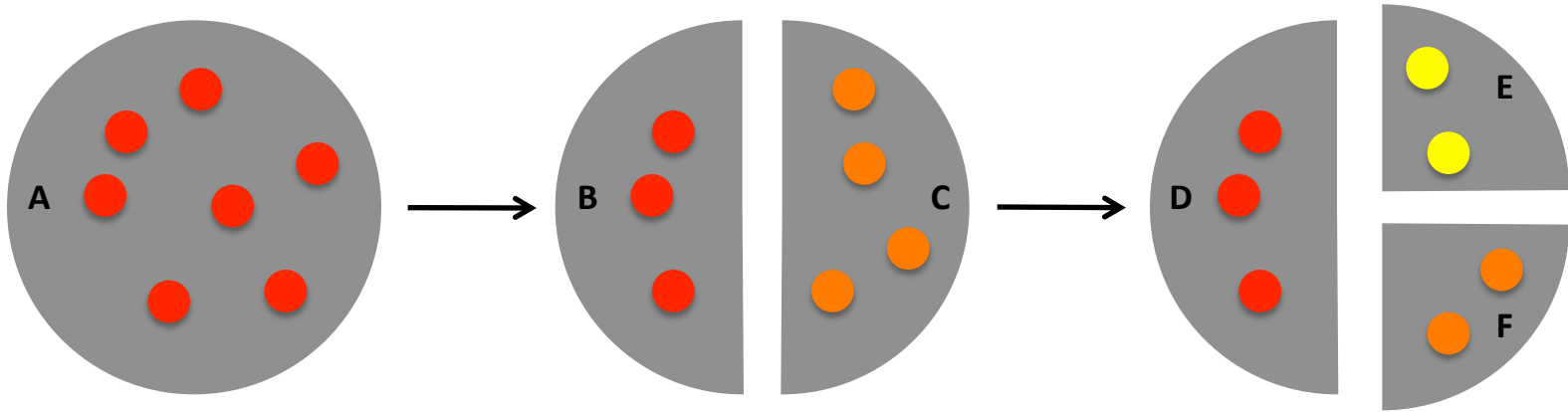
(B)



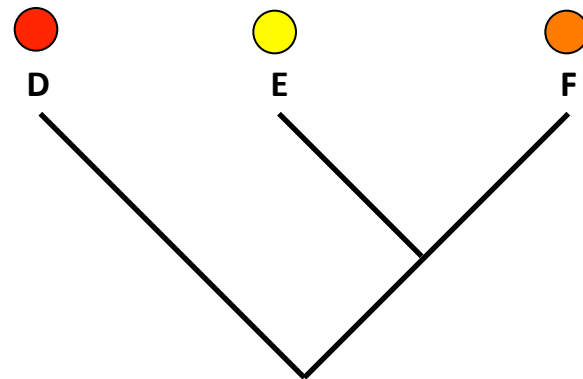
Phylogenetic reconstruction of tribe Podomini with genera indicated above colored circles

Diagram summarizes two dispersal tracks across landmasses in southern hemisphere

Phylogenetic reconstructions and vicariance



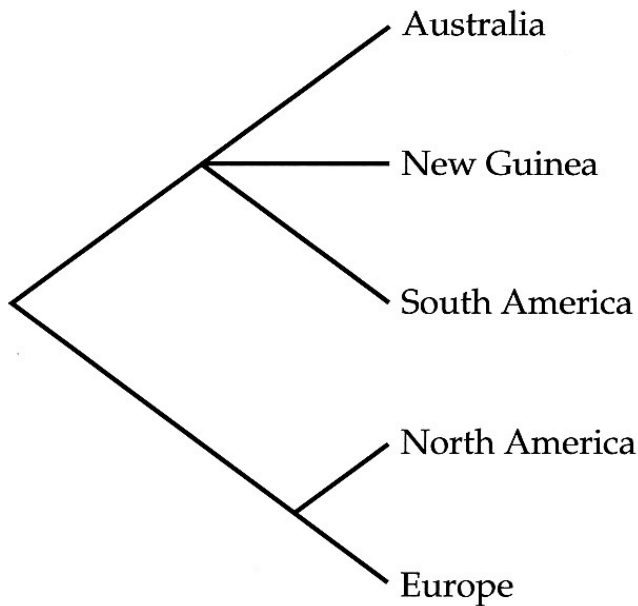
Area cladogram – labeled tree, where branches are labeled with areas



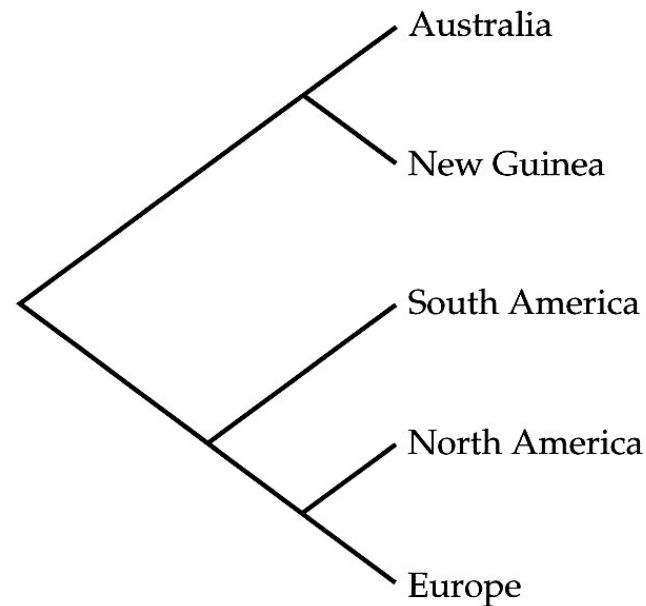
Phylogenetic reconstructions and vicariance

Consensus Area Cladogram: summary of the shared biogeographic history of multiple taxa inferred from congruent cladograms.

Consensus area cladogram for southern beech trees and midges

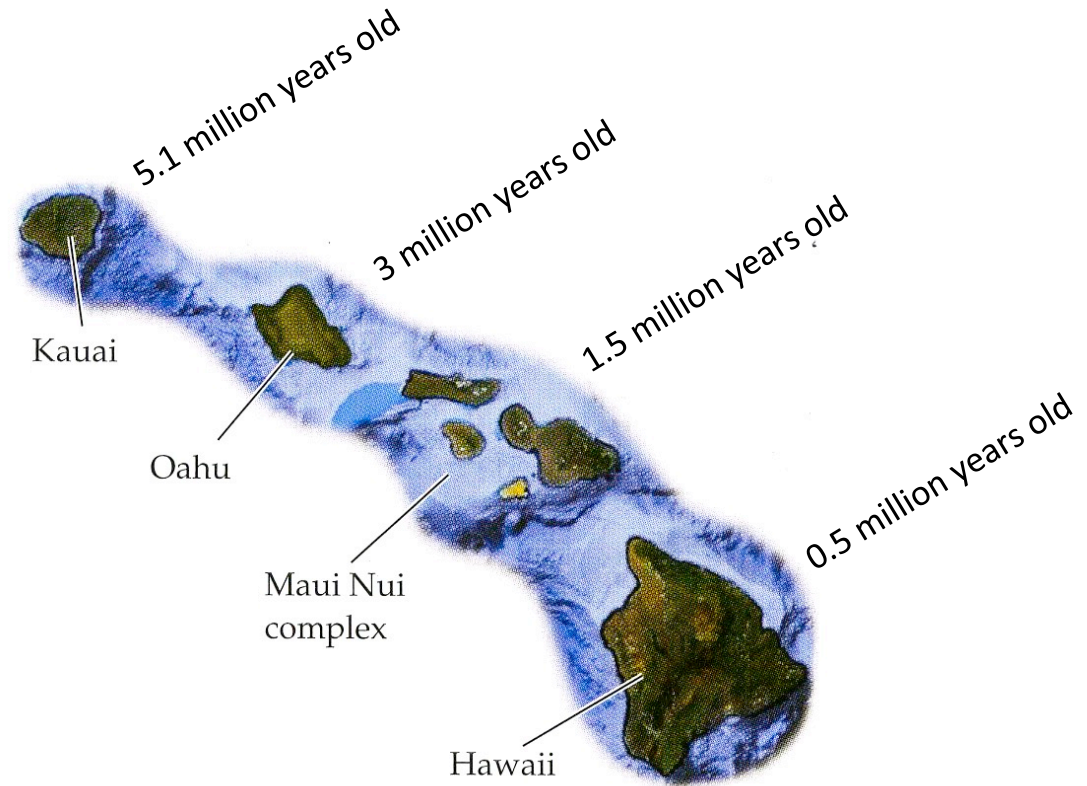


Consensus area cladogram for hylid frogs, ratite and galliform birds and xylontine fishes



Phylogenetic reconstructions and vicariance

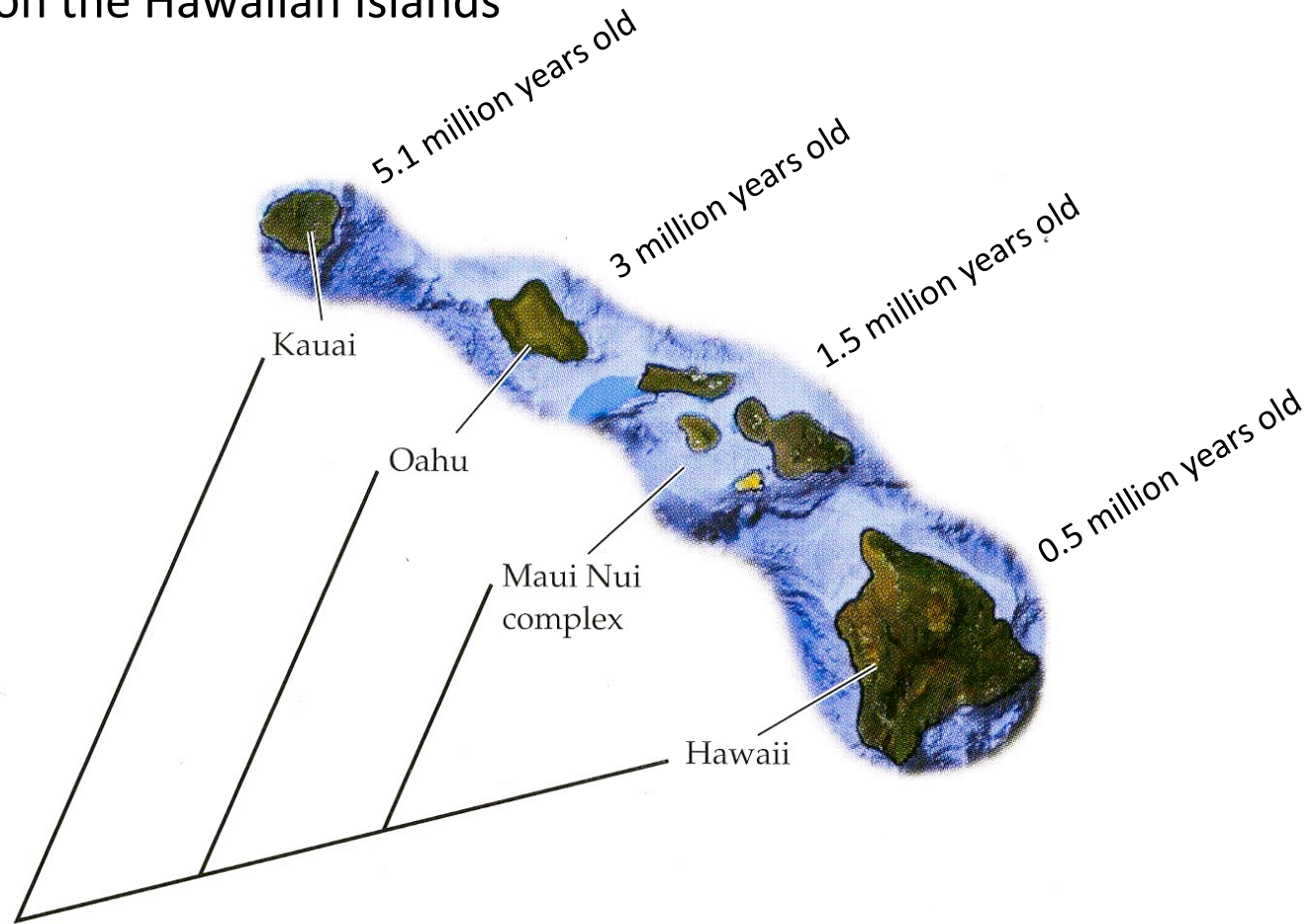
Cladogenesis on the Hawaiian Islands



(figure from Lomolino *et al.* 2010)

Phylogenetic reconstructions and vicariance

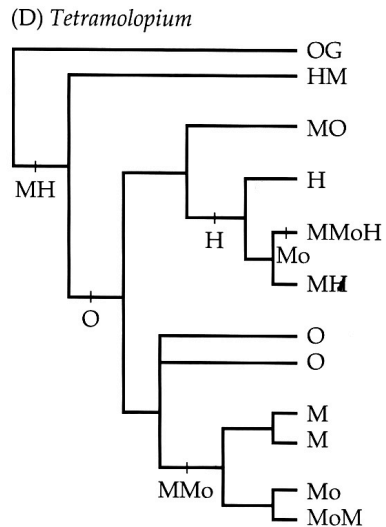
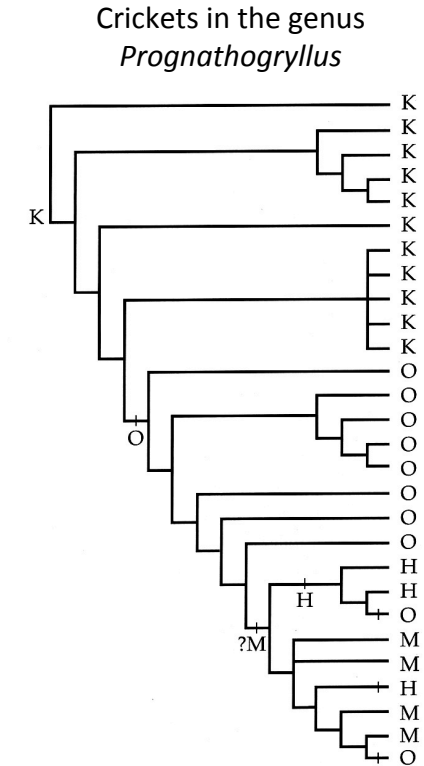
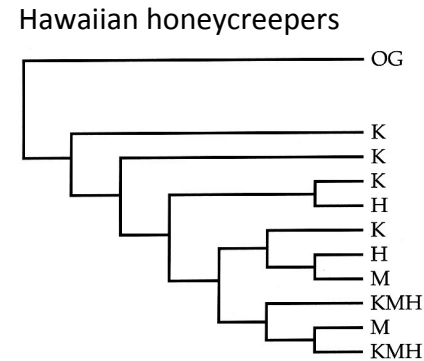
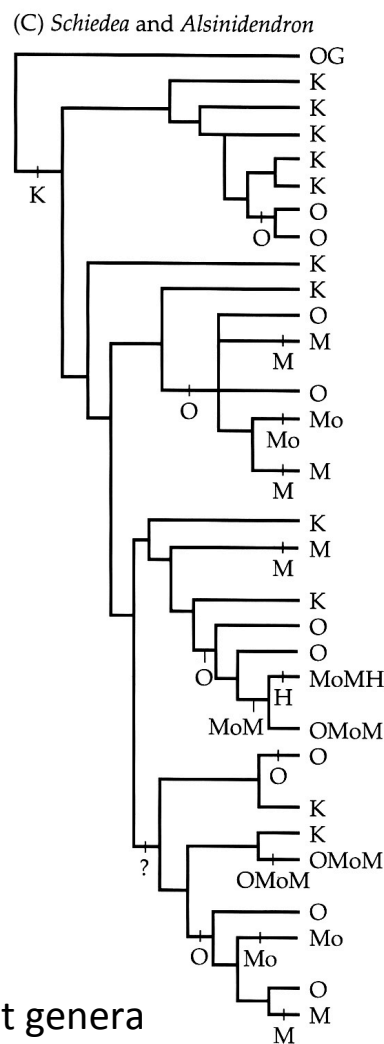
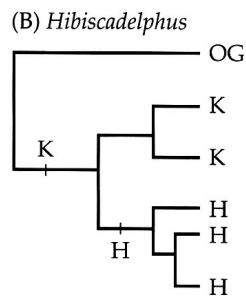
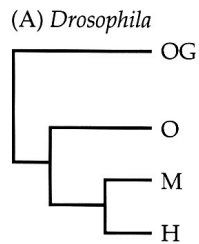
Cladogenesis on the Hawaiian Islands



(figure from Lomolino *et al.* 2010)

Phylogenetic reconstructions and vicariance

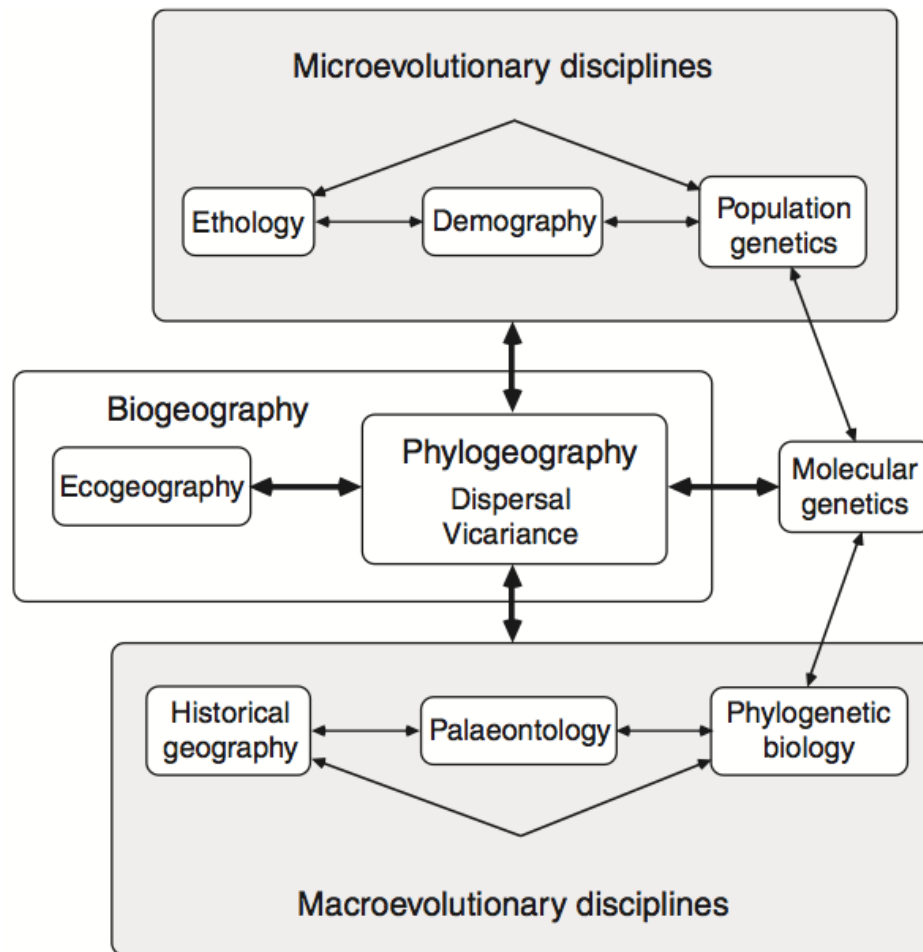
Cladogenesis on the Hawaiian Islands



(B), (C) and (D) are flowering plant genera

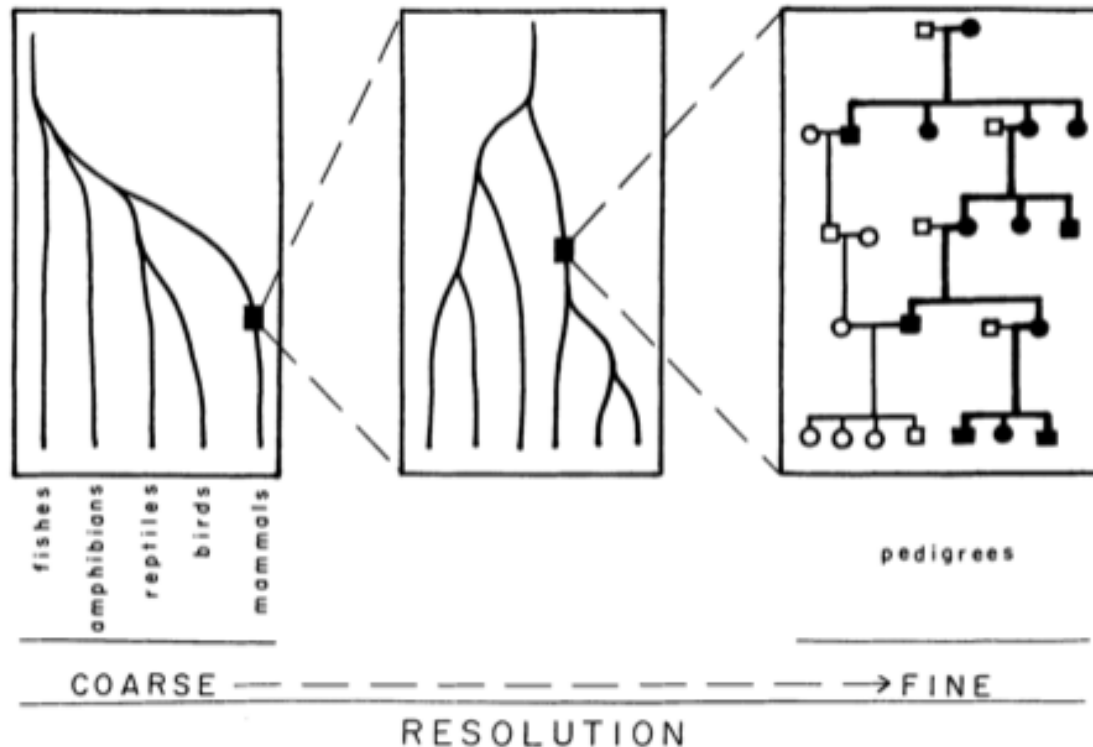
Phylogeography

Unification of *phylogenetics* with *population genetics* allowed the recognition that **microevolutionary** processes operating within species can be extrapolated to explain **macroevolutionary** differences among species and higher taxa (Avice *et al.* 1987)



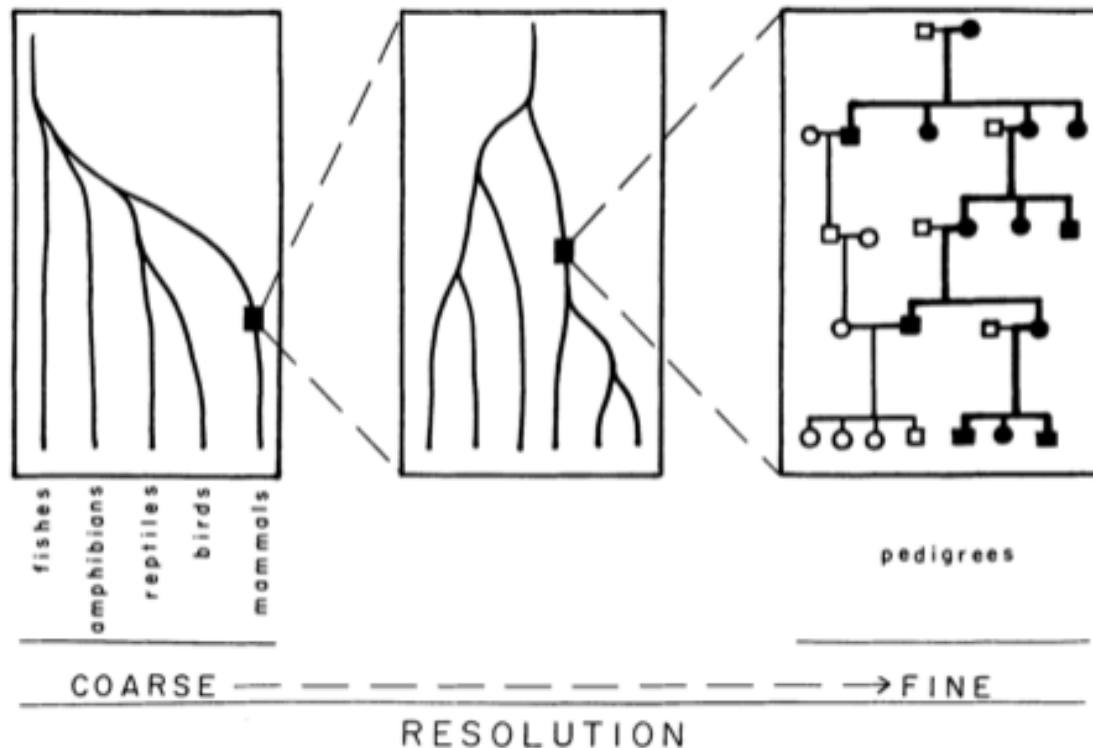
Phylogeography

Phylogeography: the phylogenetic analysis of organismal data in the context of the geographical distribution of the organism. The phylogenetic analysis of geographically-contextualized genetic data for testing hypotheses regarding the causal relationship among geographic events, demographic events, species distributions, and speciation. (Hickerson *et al.* 2010)



Phylogeography

Phylogeography: An approach in historical biogeography that studies the geographic distribution of genealogical lineages, within species and among similar species, and attempts to differentiate between historical and ongoing processes leading to the development of observed patterns. (Lomolino *et al.* 2010)



Phylogeography

Extensive use of mtDNA

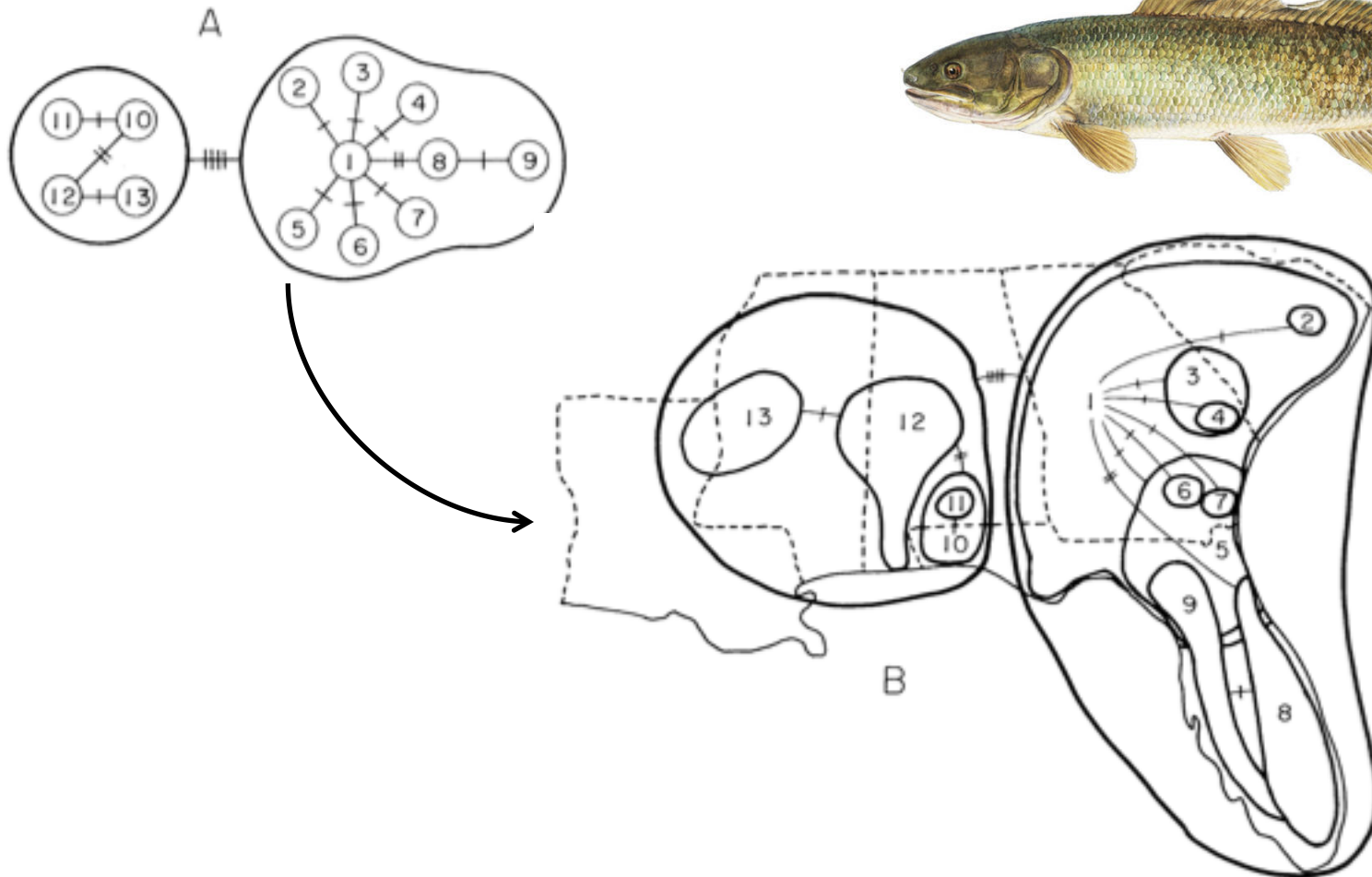
Why is mtDNA so often used in phylogeography?

- lack of recombination (especially intragenic)
- haploid
- selectively neutral variation (maybe)
- small effective population size
- rapid evolution (in animals)
- many copies per cell

(shorter expected time to reciprocal monophyly between geographic regions compared to nuclear DNA)

Phylogeography

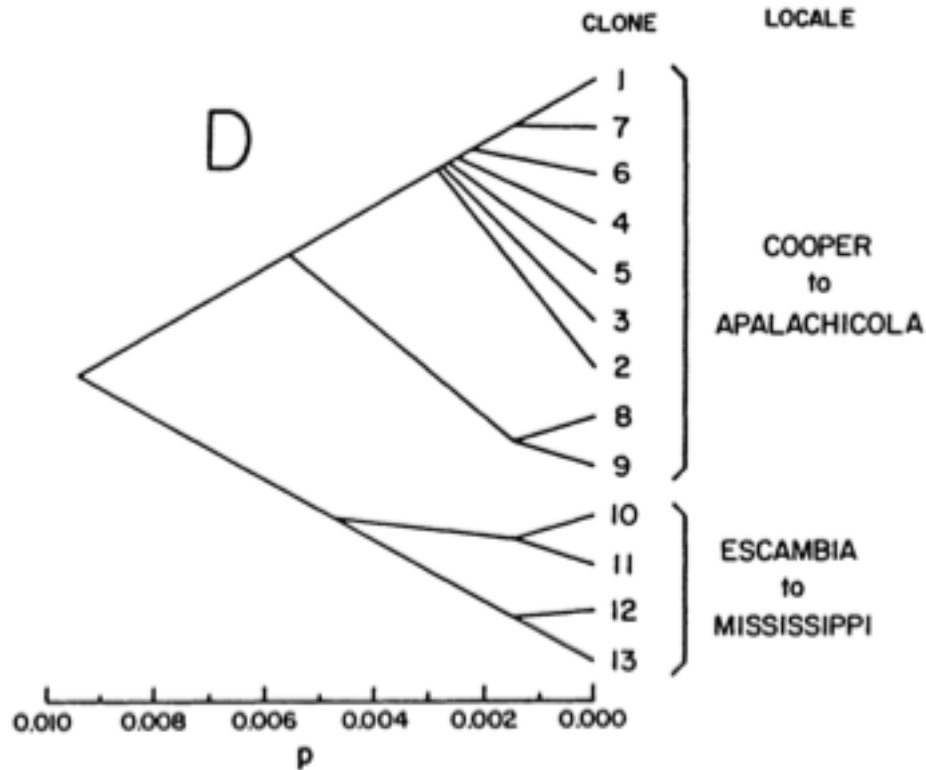
Southeastern North America



Haplotype network (based on parsimony) showing evolutionary relationships among 13 mtDNA genotypes observed in a sample of 75 bowfin fish, *Amia calva* (Avice 1987).

Phylogeography

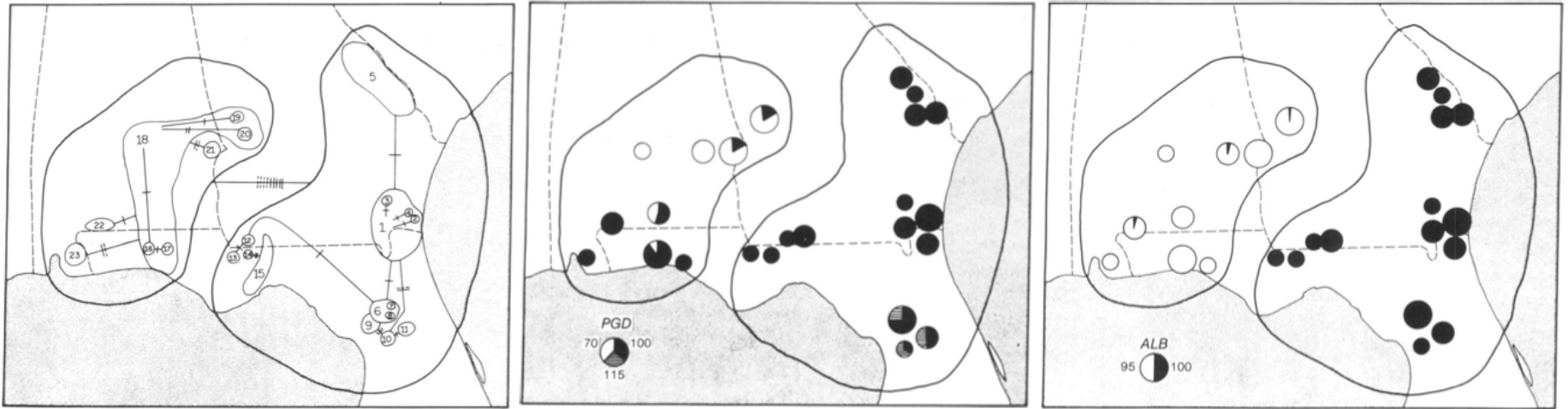
Southeastern North America



Phylogeny showing evolutionary relationships among 13 mtDNA genotypes observed in a sample of 75 bowfin fish, *Amia calva*, where P is estimated sequence divergence (Avice 1987)

Phylogeography

Southeastern North America



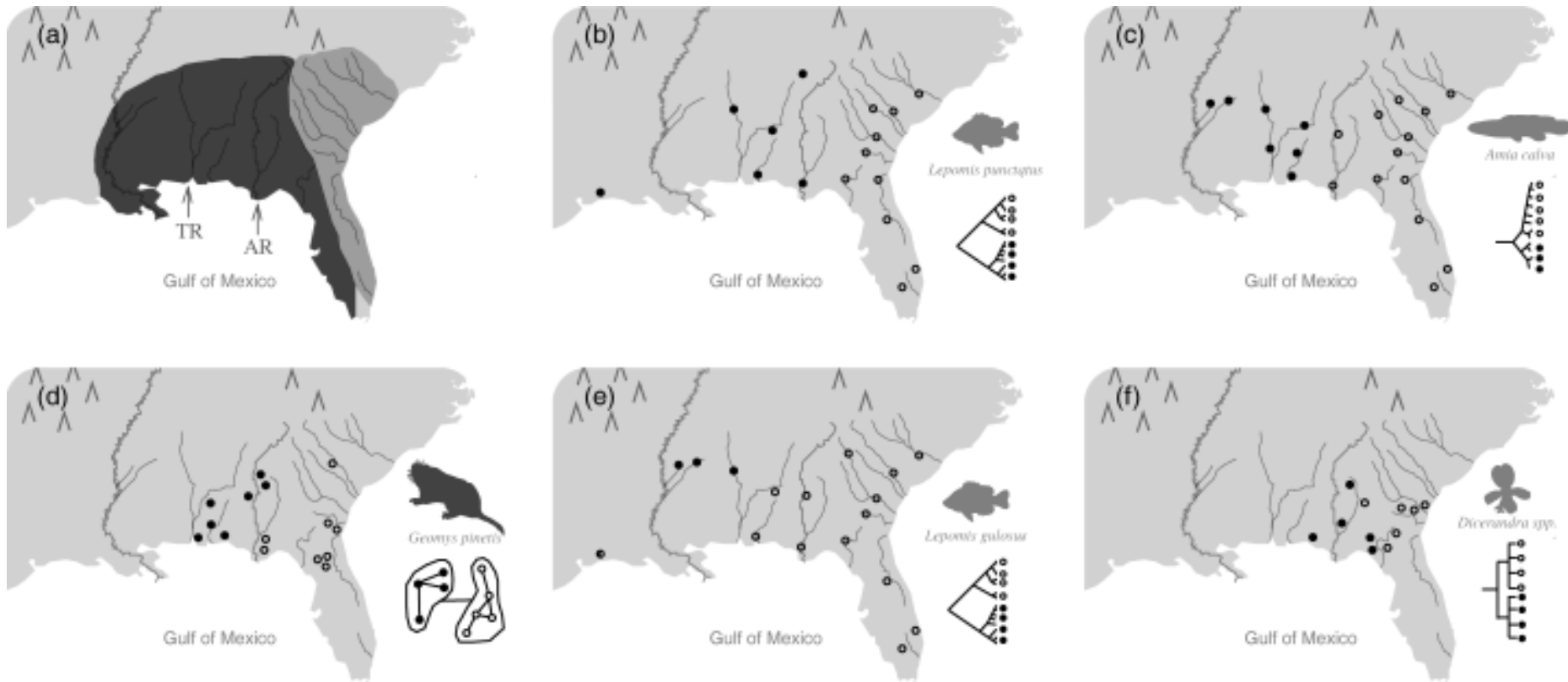
Geographic distribution of mtDNA haplotypes and nuclear-encoded protein electromorphs of southern pocket gophers, *Geomys pinetis* (Avise *et al.* 1979).

This study examined several different kinds of genetic evidence to see whether they reflected similar biogeographic divides in the pocket gophers.



Phylogeography

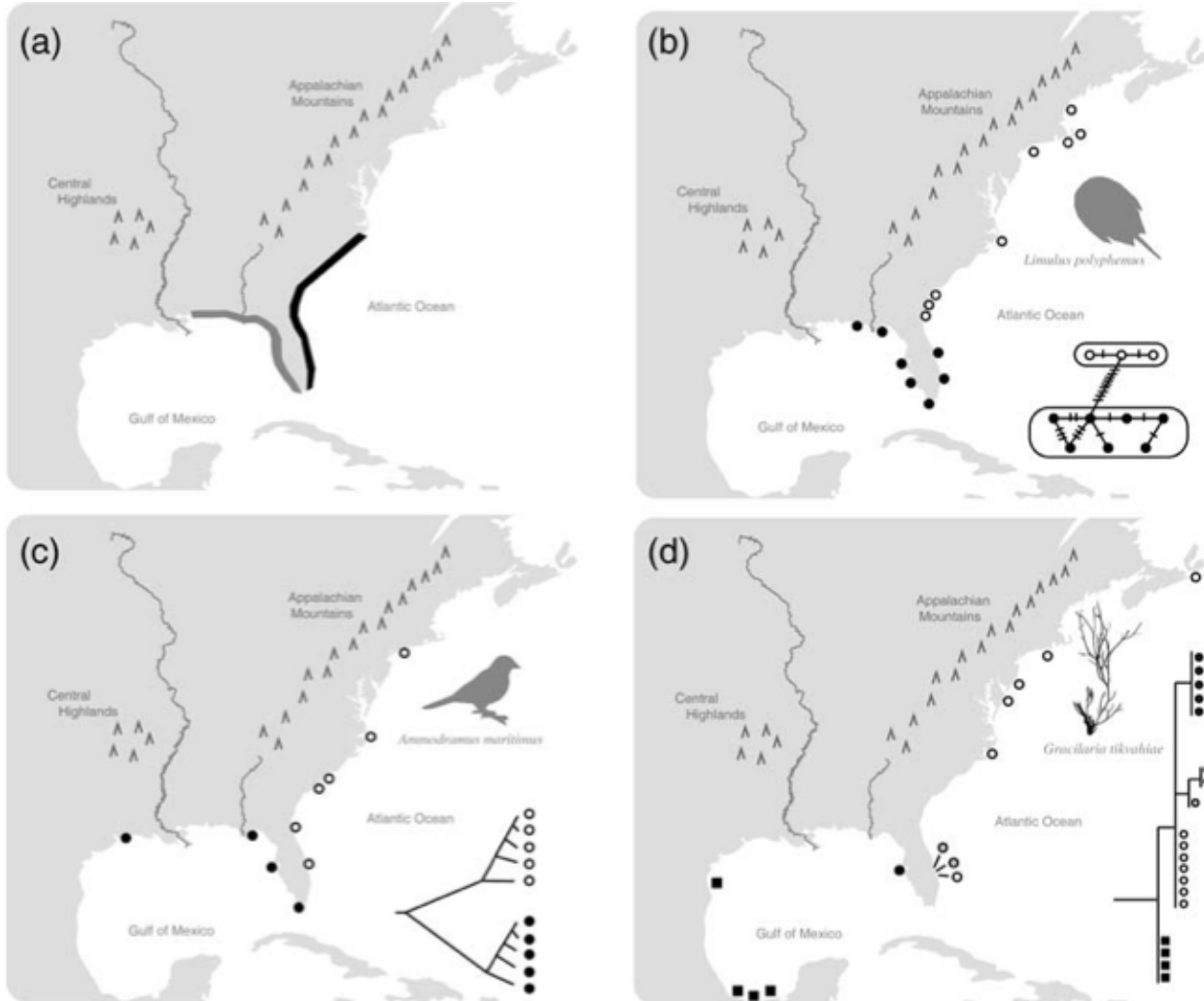
Southeastern North America



Congruent discontinuities in the distributions of spotted sunfish, bowfin, pocket gopher, warmouth sunfish, and the coastal plain balm, corresponding to Apalachicola (AR) and Tombigbee River (TR) drainages (Soltis *et al.* 2006).

Phylogeography

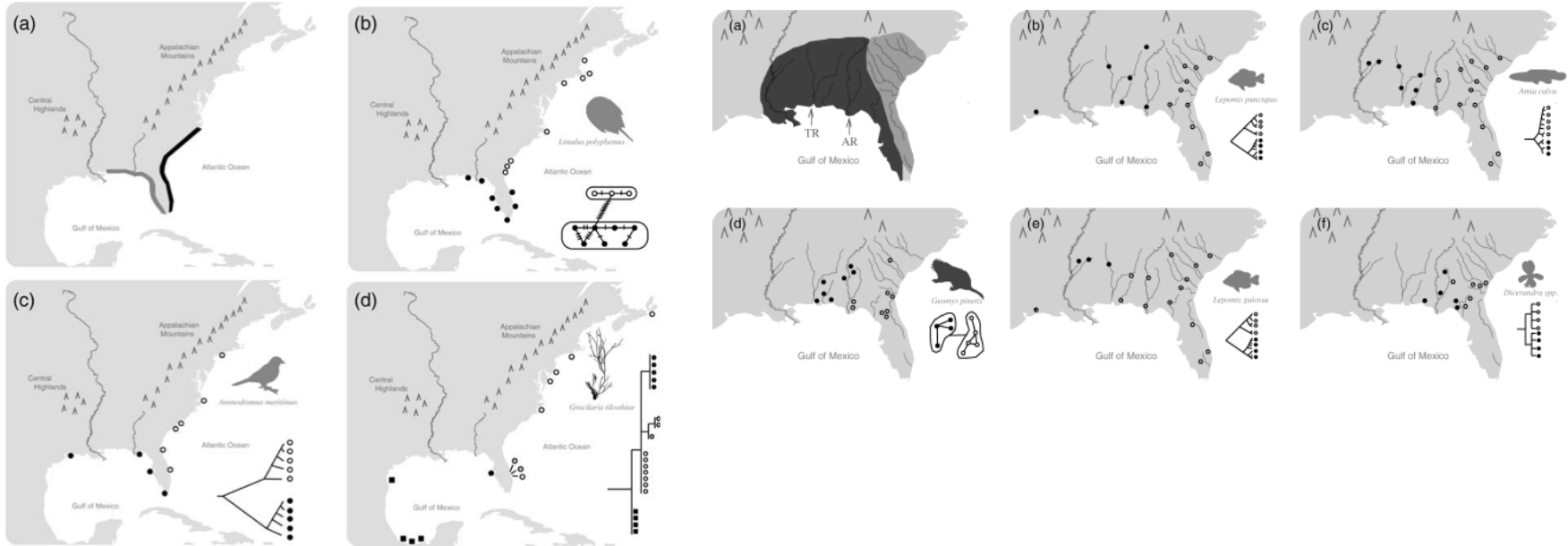
Southeastern North America



Congruent discontinuities in the distributions of Horseshoe crab, dusky seaside sparrow, and the red alga, *Gracilaria tikvahiae* (Soltis *et al.* 2006).

Phylogeography

Southeastern North America



Soltis *et al.* 2006 showed that similar patterns, initially documented in animals, are also apparent in plants and broad taxonomic groups, providing support for phylogeographical generalizations.

Statistical Phylogeography

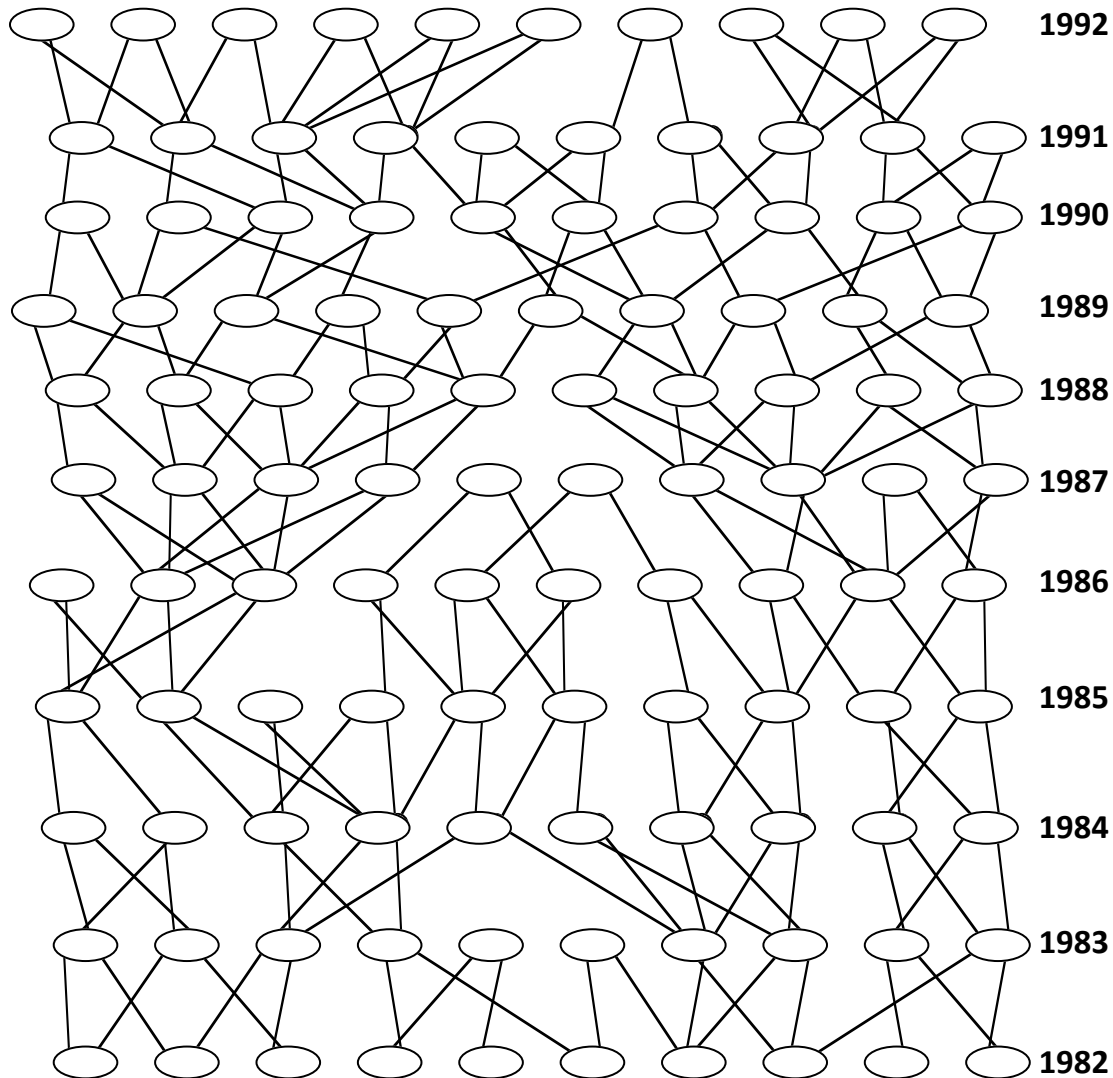
Statistical Phylogeography: The framing of phylogeographic investigations within a rigorous statistical framework through development of alternative hypotheses.

Several statistical frameworks are used, but a common and more widely utilized method is based upon coalescent theory:

Coalescence: In a gene tree, the point in time (absolute time or scaled to generations) at which two allelic lineages diverged from an ancestral lineage.

Coalescence

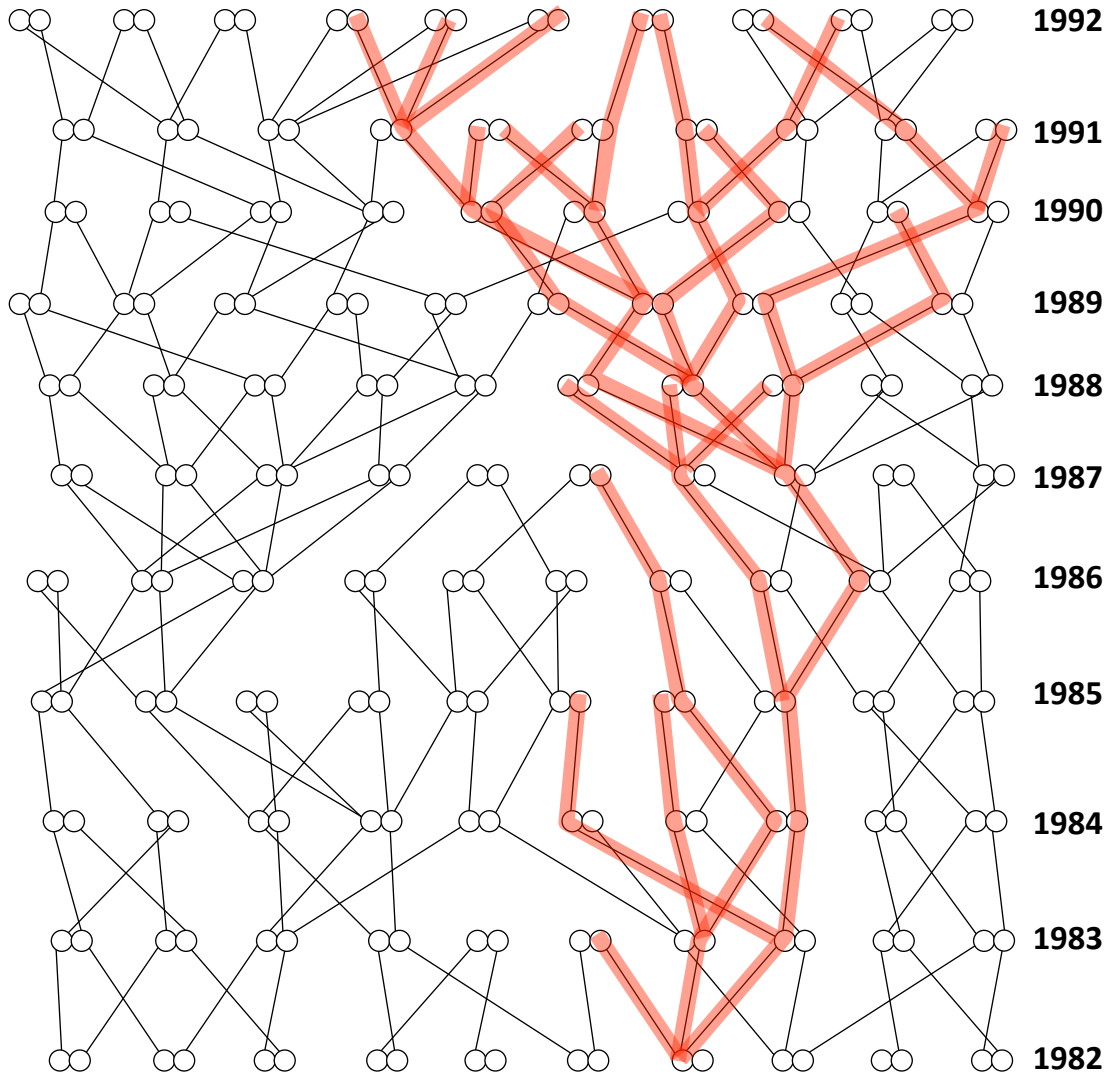
Gene Tree: history of one gene (or of one genetic locus)



Coalescent theory relates patterns of common ancestry to population size and structure

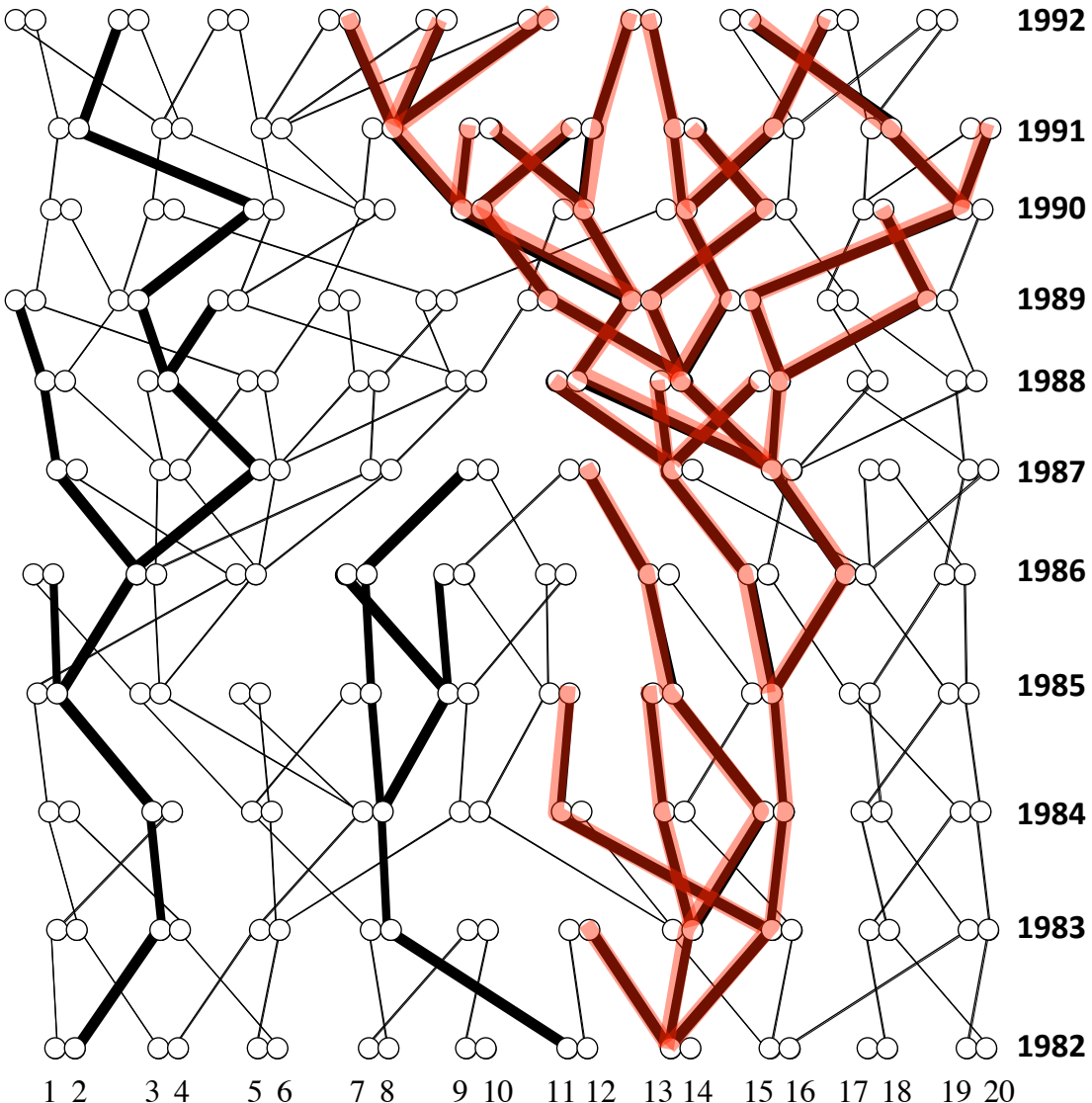
Coalescence

Gene Tree: history of one gene (or of one genetic locus)



Coalescence

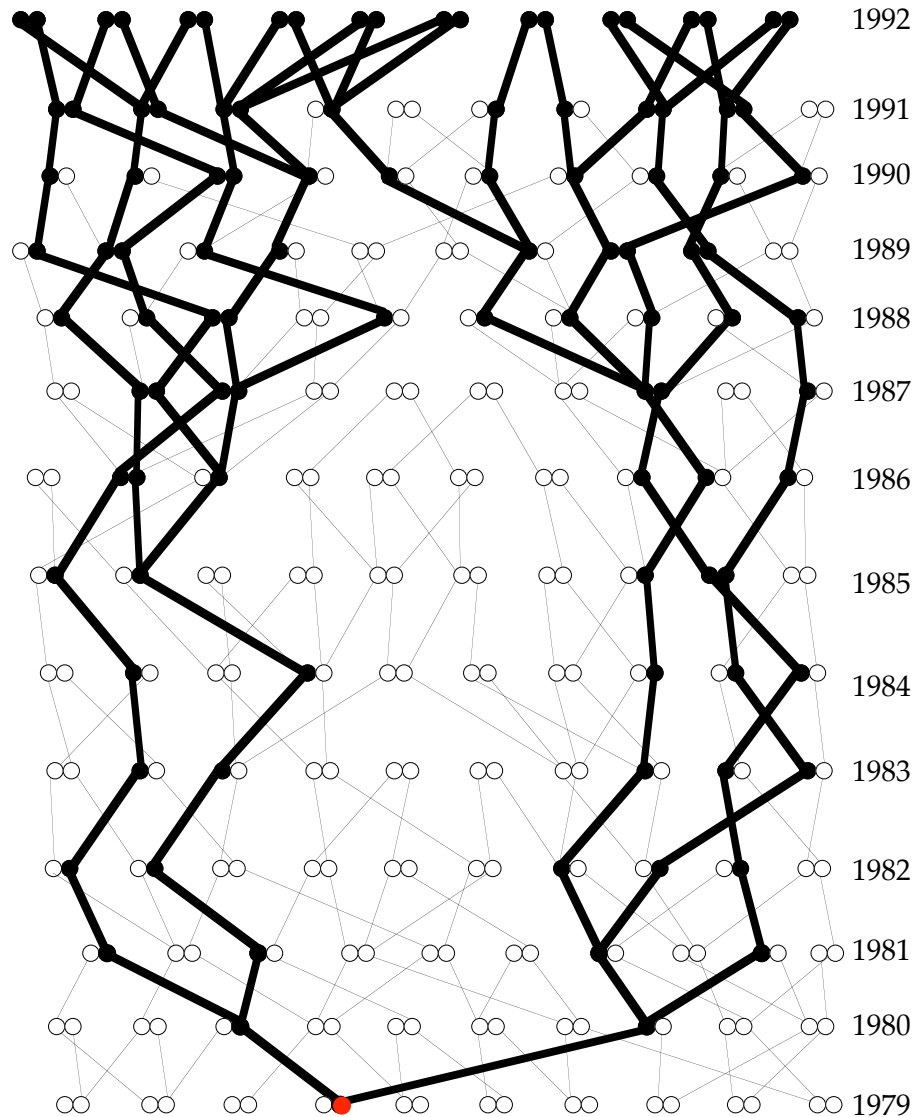
Gene Tree: history of one gene (or of one genetic locus)



Each copy's descent is a tree because at each generation the copy might have many descendants, but will only have a single ancestor

Coalescence

Gene Tree: history of one gene (or of one genetic locus).



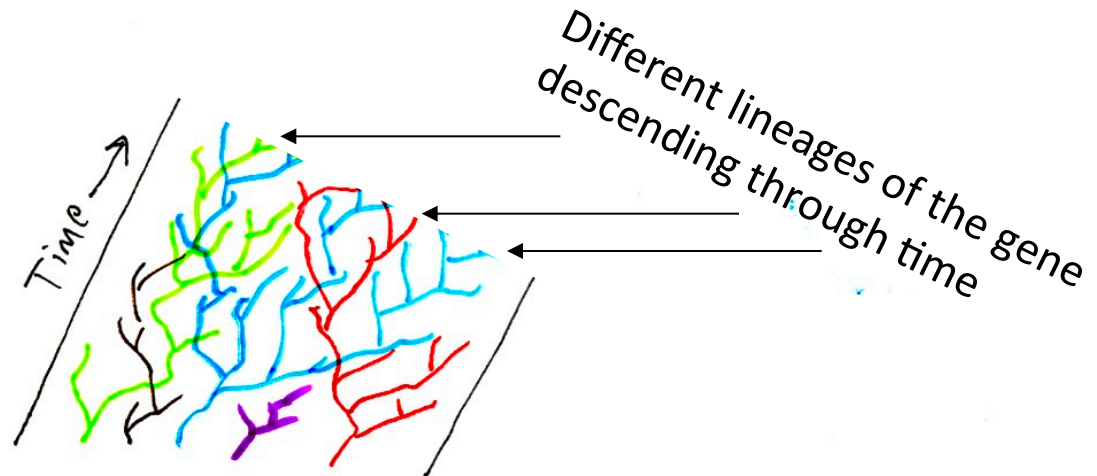
Looking backward in time, sooner or later we'll get to a single copy that was ancestor of all extant copies.

Looking backward in time, we say the gene copies have **coalesced** to a single ancestor.

Coalescence

Gene Tree: history of one gene (or of one genetic locus)

At any given time, a population has many genes competing for success.

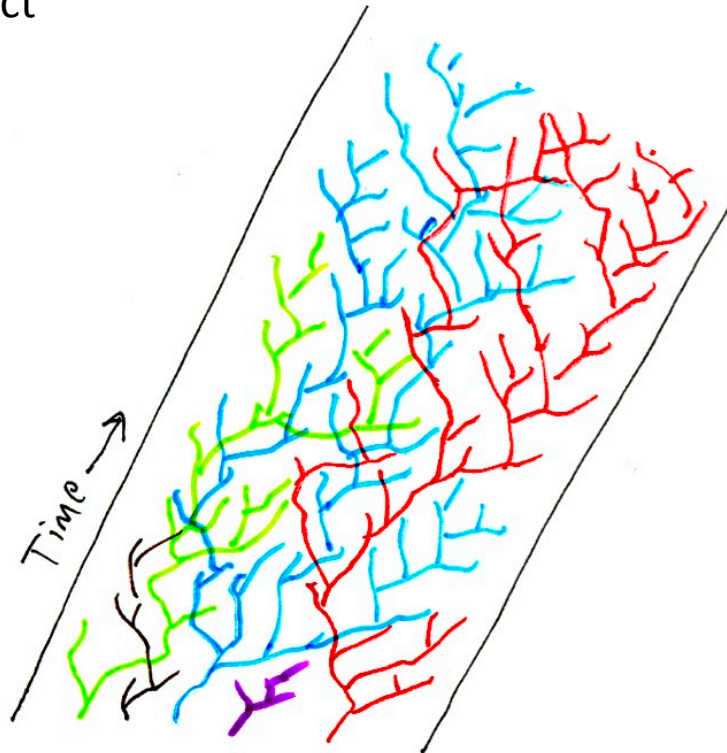


Coalescence

Gene Tree: history of one gene (or of one genetic locus)

At any given time, a population has many genes competing for success.

Some lineages will go extinct by drift (i.e., bad luck).

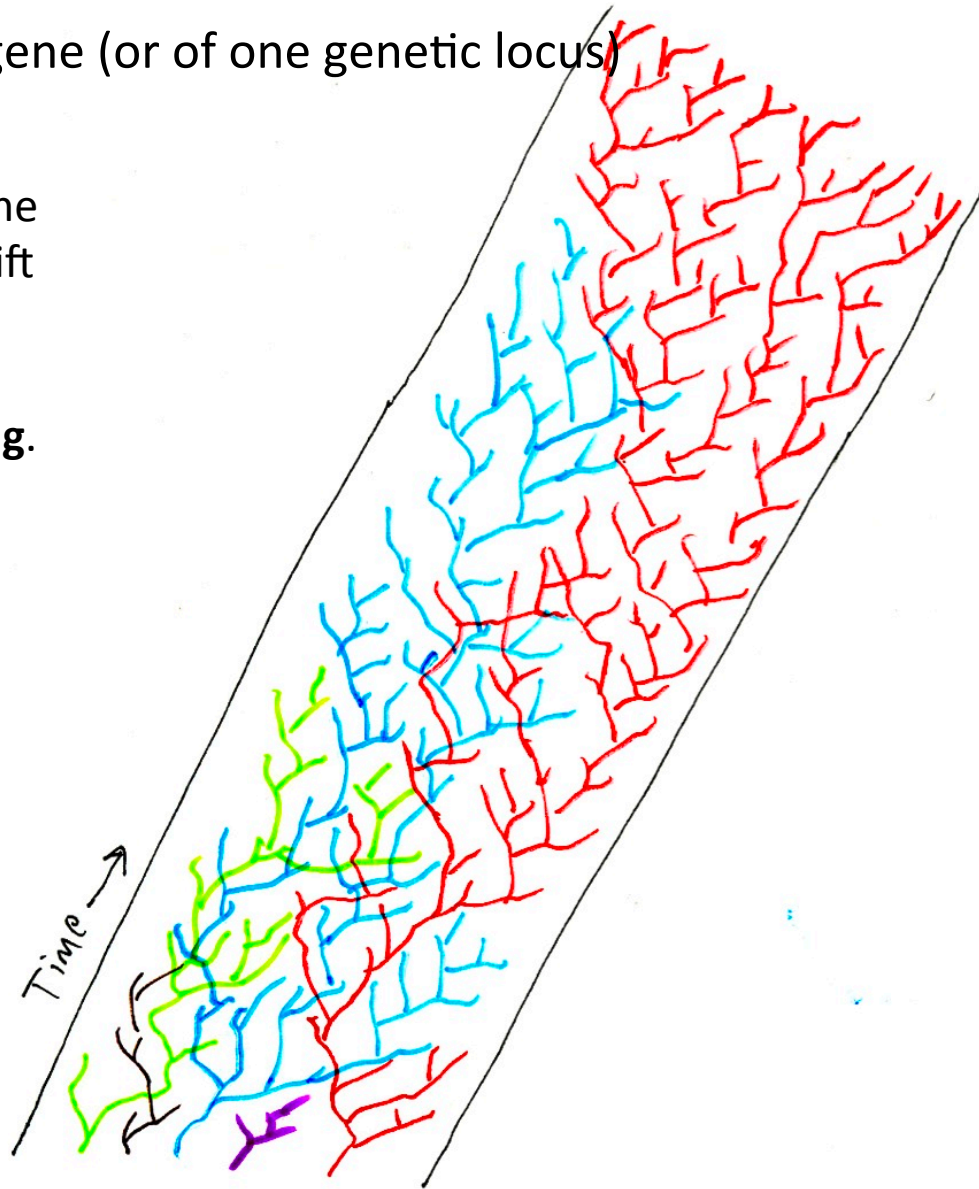


Coalescence

Gene Tree: history of one gene (or of one genetic locus)

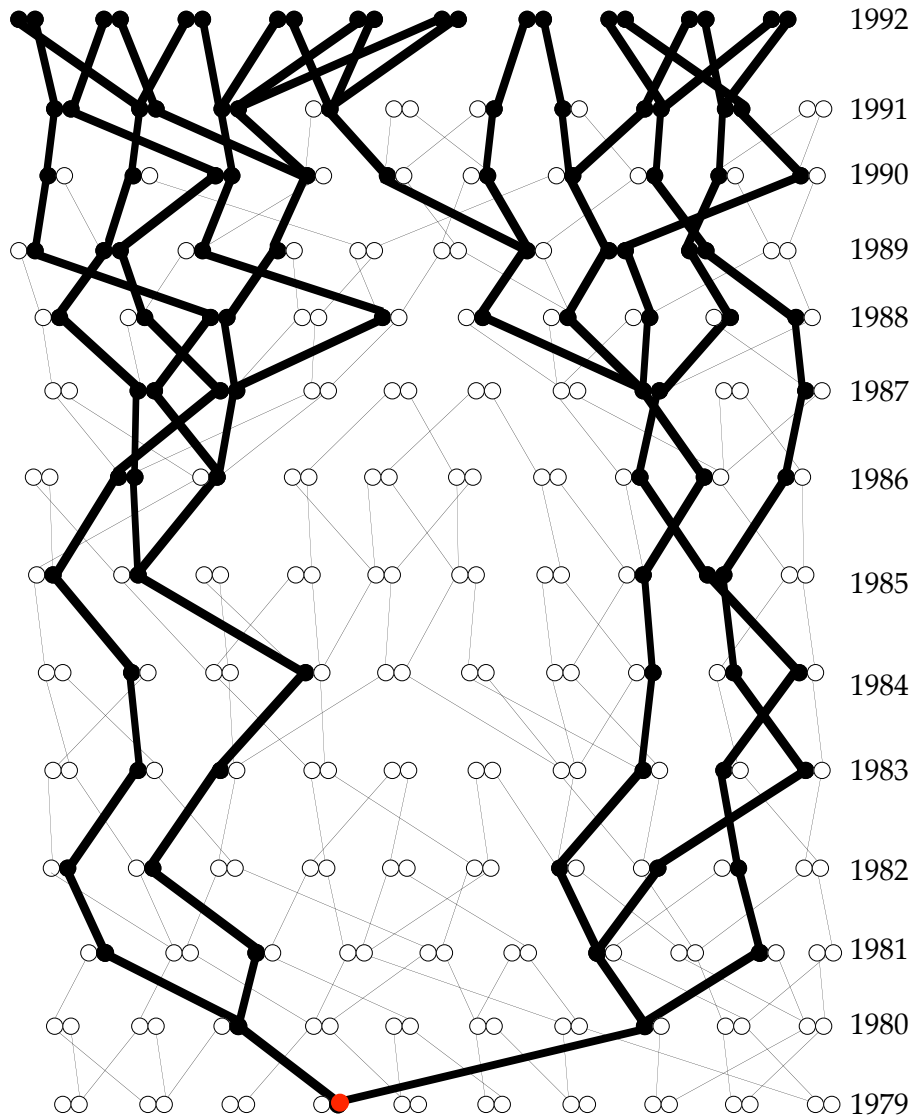
Given enough time, only one lineage will remain (i.e., drift will cause **fixation**).

This is called **lineage sorting**.



Coalescence

Gene Tree: history of one gene (or of one genetic locus)



Average time until fully coalesced (i.e. single ancestral copy):

Diploid, population size of N individuals: $4N$ generations

Haploid, population size of N individuals: $2N$ generations

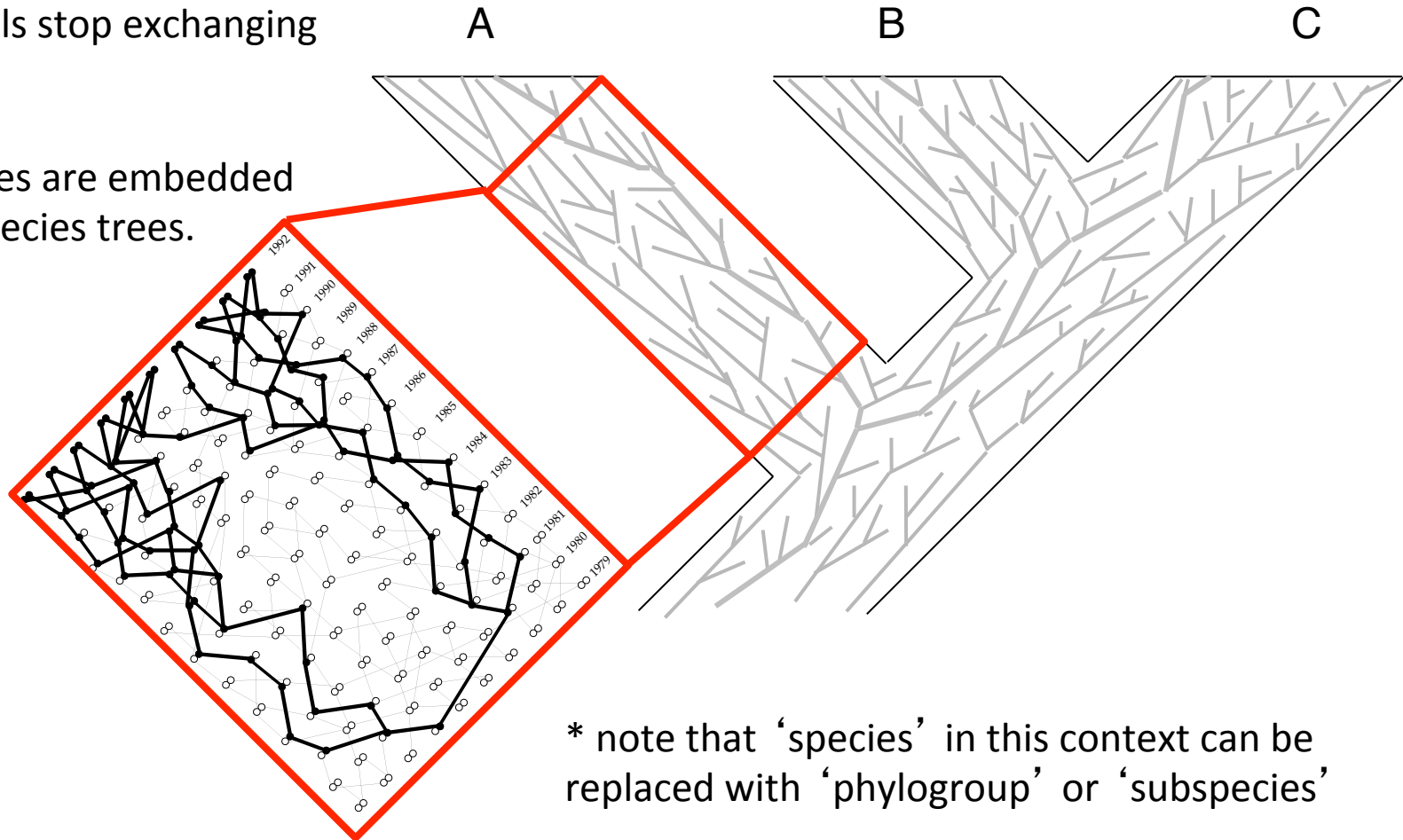
The bigger the population, the longer until coalescence.

Coalescence

Species Tree: history of related species*.

Species arise when groups of individuals stop exchanging genes.

Gene trees are embedded within species trees.



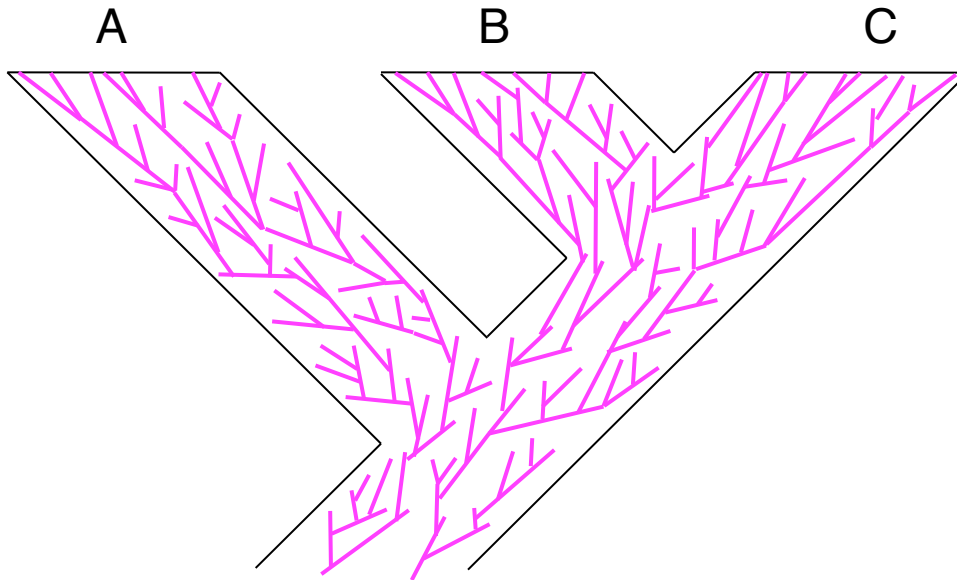
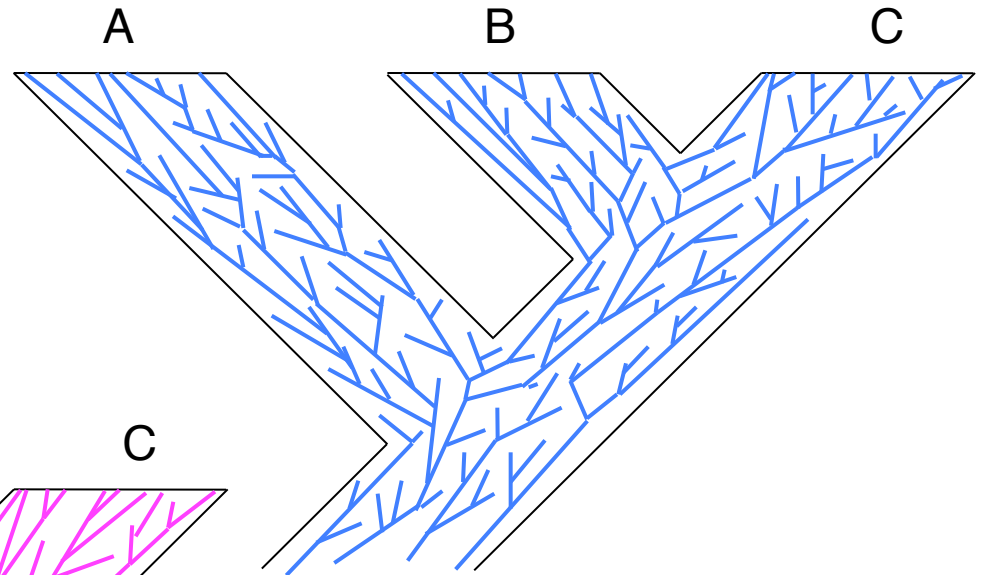
* note that 'species' in this context can be replaced with 'phylogroup' or 'subspecies'

Coalescence

Species Tree: history of related species*.

Even within the same set of species, different loci will have different gene trees.

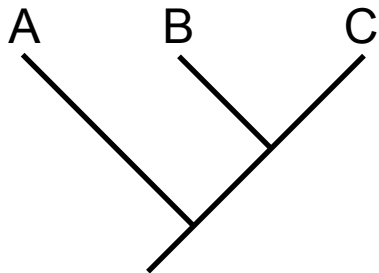
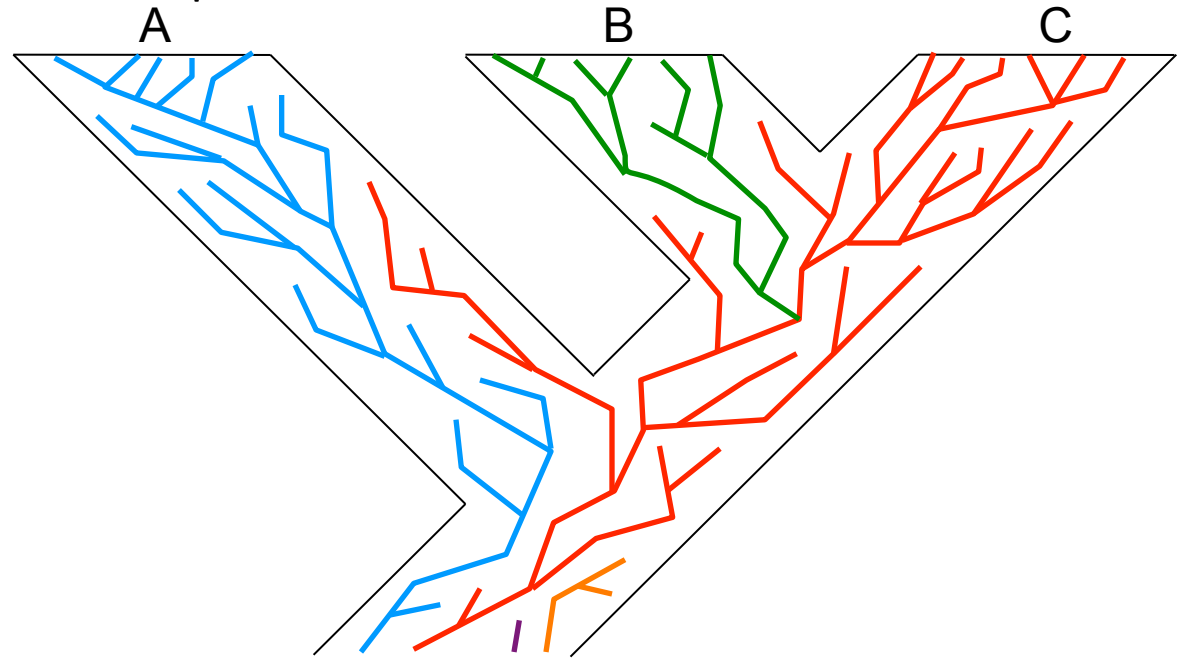
The pattern of coalescence (and the inferred species history) will depend on which gene locus is analyzed.



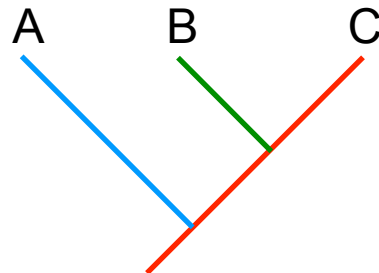
Coalescence

Species Tree: history of related species*.

This gene reflects the species history:



Species tree



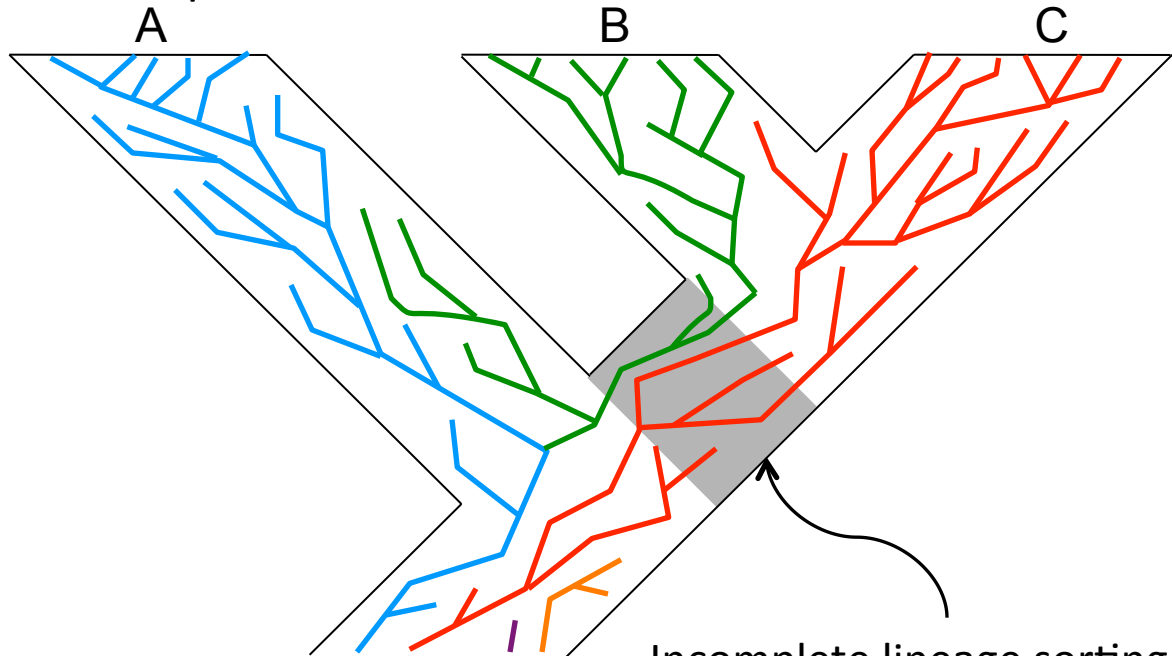
Gene tree

Coalescence

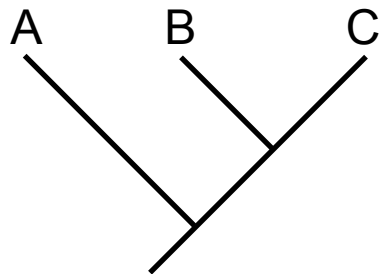
Species Tree: history of related species*.

This gene does not reflect the species history:

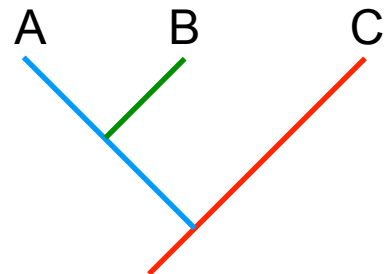
This is called **incomplete lineage sorting**.



Incomplete lineage sorting occurs when time between species divergences is short compared to the population size (short and wide branches)



Species tree



Gene tree

Revisiting phylogenetic reconstructions

Because gene trees do not always reflect species trees, robust phylogenetic reconstruction typically uses multiple genes (mitochondrial and nuclear)

Using many genes gives multiple lines of evidence on species evolutionary relationships

Example: Phylogeny of ovenbirds and woodcreepers (avian family Furnariidae) utilized three mitochondrial genes and three nuclear genes.

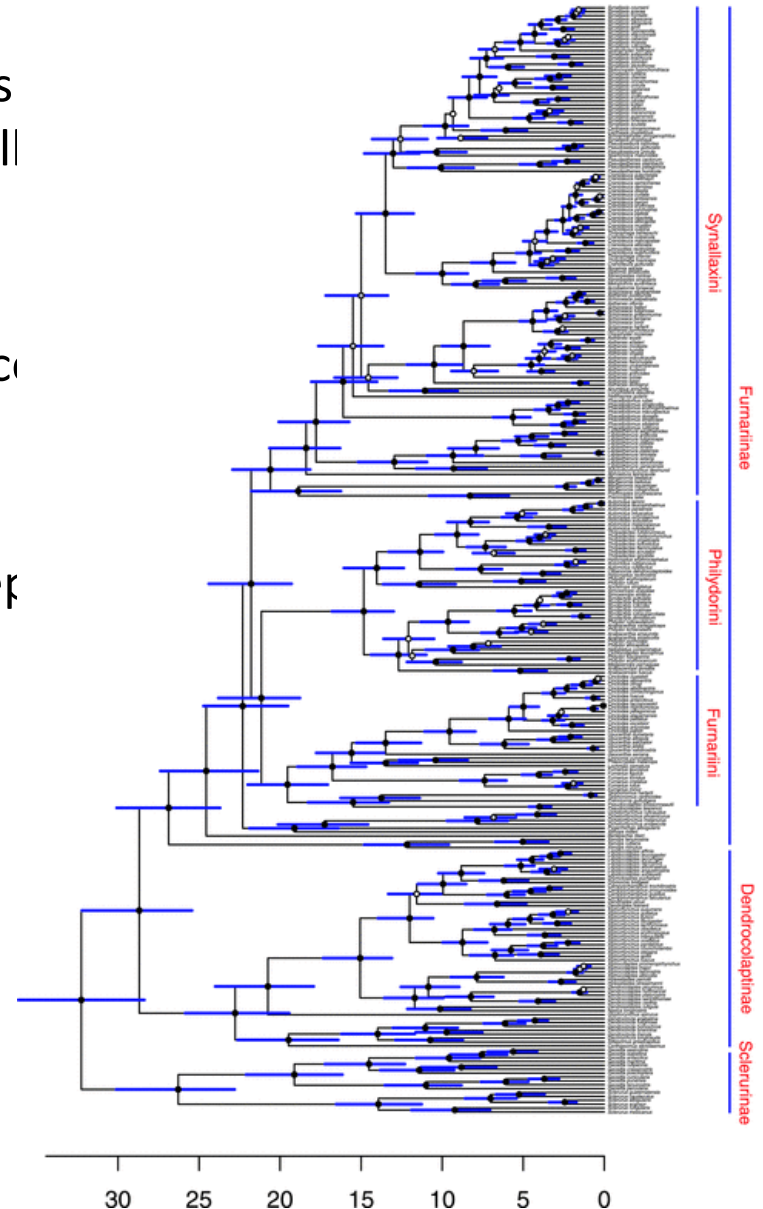


Striped Woodcreeper



Black-billed Woodcreeper

Figure 1 from Derryberry et al. 2011



Evolutionary lineages and phylogenetics

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