

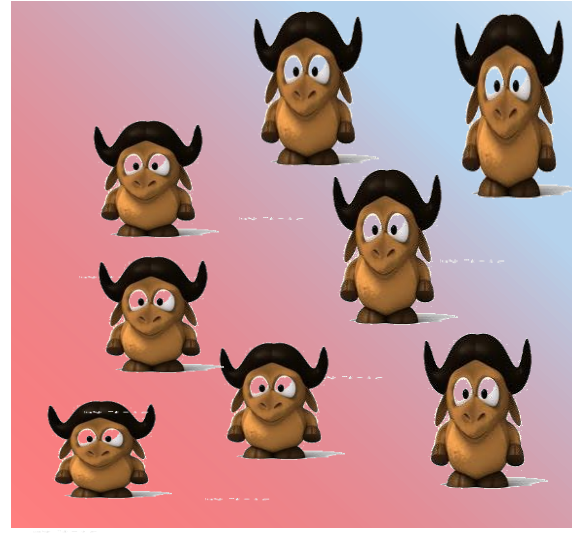
Evolution, phylogeny and classification. Cladistics. Properties and uses of phylogenetic trees



Life: discrete or continuous?



Comte de Buffon (1707-1788)



Cuvier (1769-1832)

Organisms occupy different areas of a continuum **vs.** Organisms represent a finite number of constant types

Both visions result from human perception on biodiversity. This perception needs to be explained by science

Although the sort of questions we pose today are different, the issue on the “reality” of boundaries is still surprisingly problematic

Classification as a tool for understanding

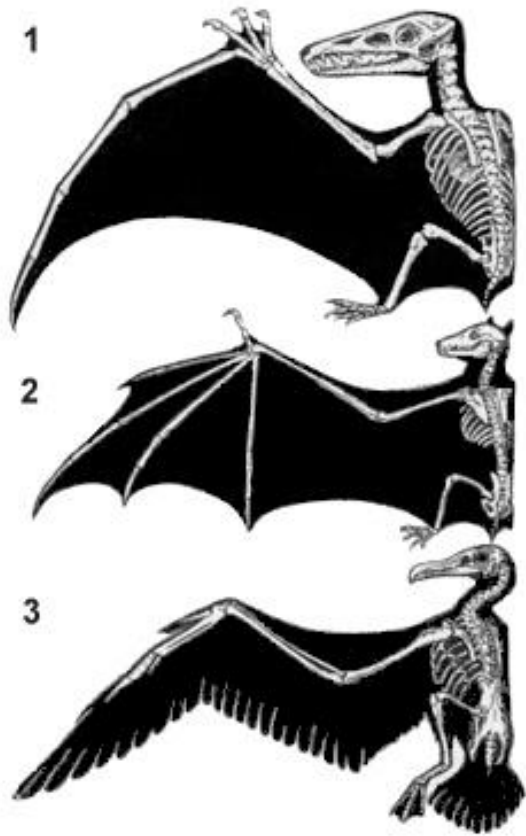
Classification may be the result of a pragmatic need, but from a scientific point of view, mankind has aimed for a “natural” classification of organisms based on their intrinsic characteristics

That “natural” classification however, turned out to be very tricky and full of conflicts due to the different sources of **similarity** (lumping criteria) among organisms

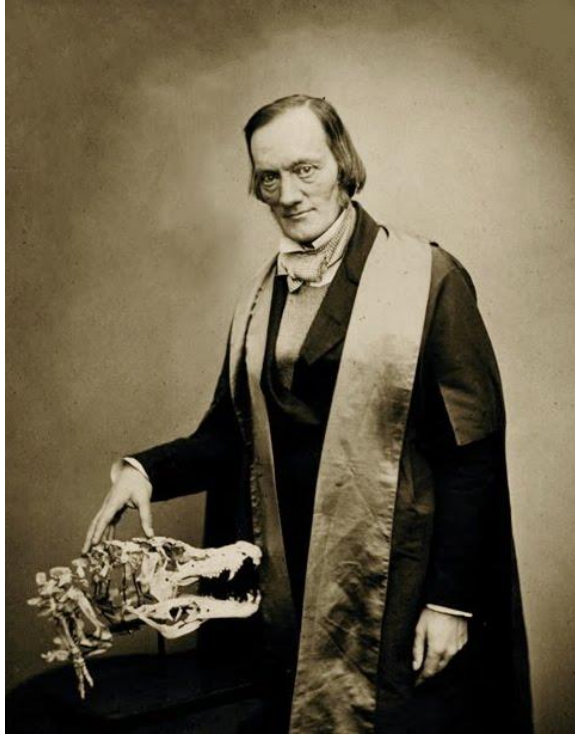


Similarity can be tricky

However, since the beginning of the search for a comprehensive natural classification, taxonomists perceived that there were **different kinds of similarity**, and some of them were more relevant than others



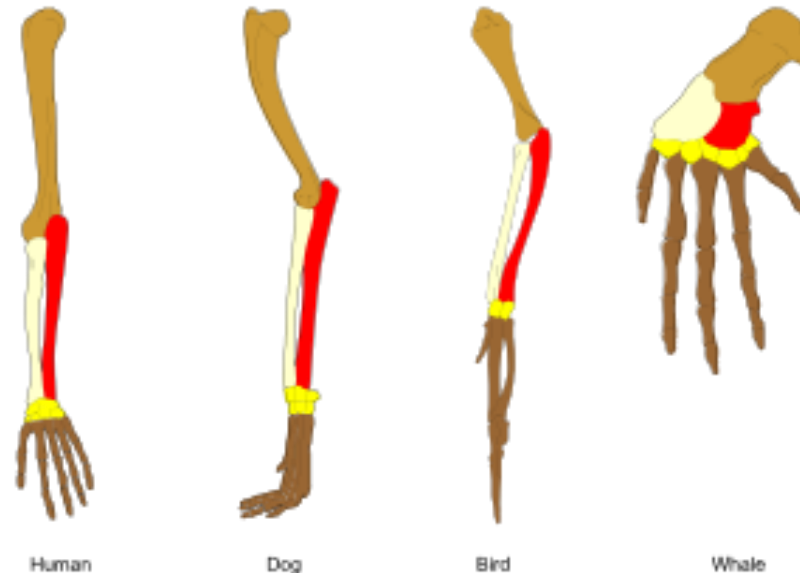
Homology: the key concept



Richard Owen (1804-1892)

The expertise of the most lucid morphologists allowed them to distinguish between **homology** and **homoplasy**

Homology: similarity derived from the modification of, essentially, the same structural element in the anatomy of an organism



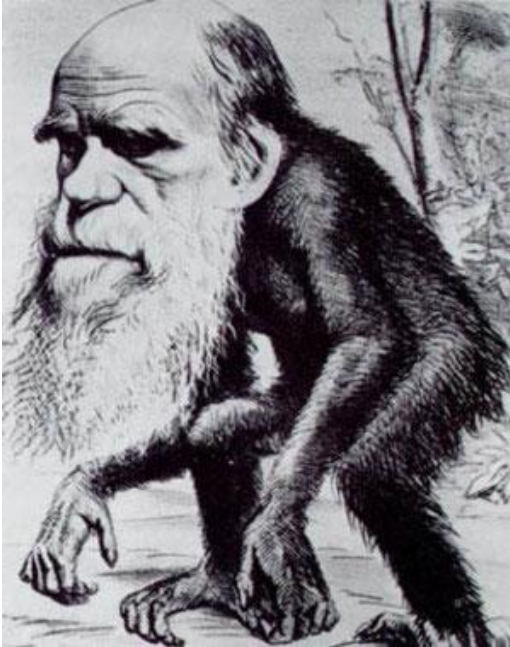
Homoplasy: the evil sister

Homoplasy: similarity derived from a superficial resemblance of structural elements that are not truly equivalent



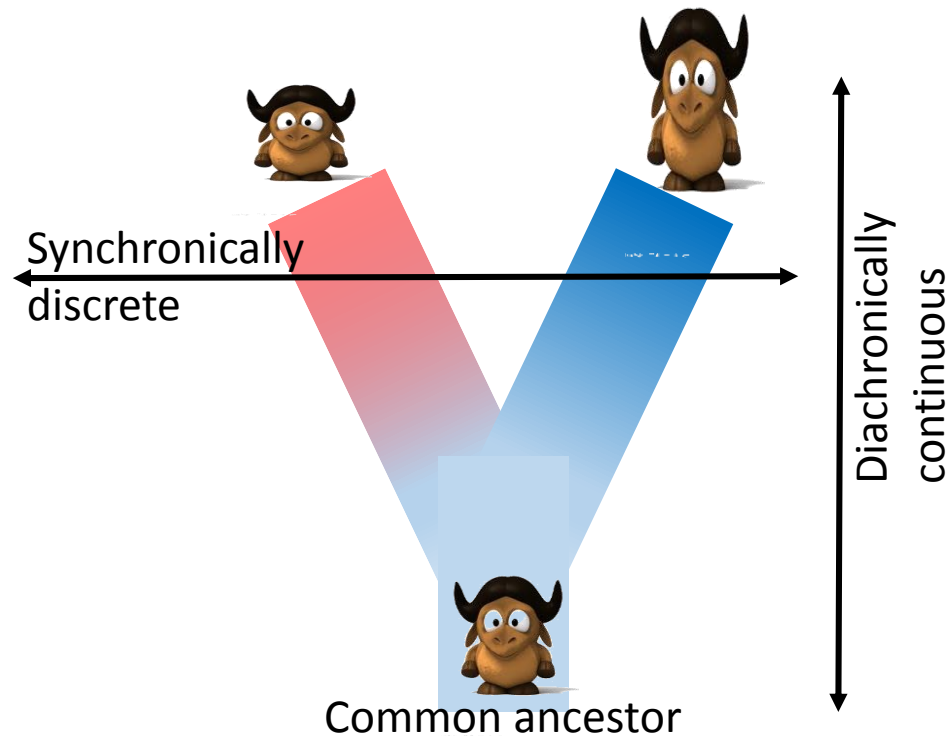
Frank Vincentz

Descent with modification: the meaning of homology



Charles Darwin (1809-1882)

Pre-evolutionary morphologists knew quite well *what* they were doing, but they did not *why* they perceived some similarities to be more relevant than others. The scientific explanation of homology is phylogenetic: two traits are homologous if they share a common ancestor

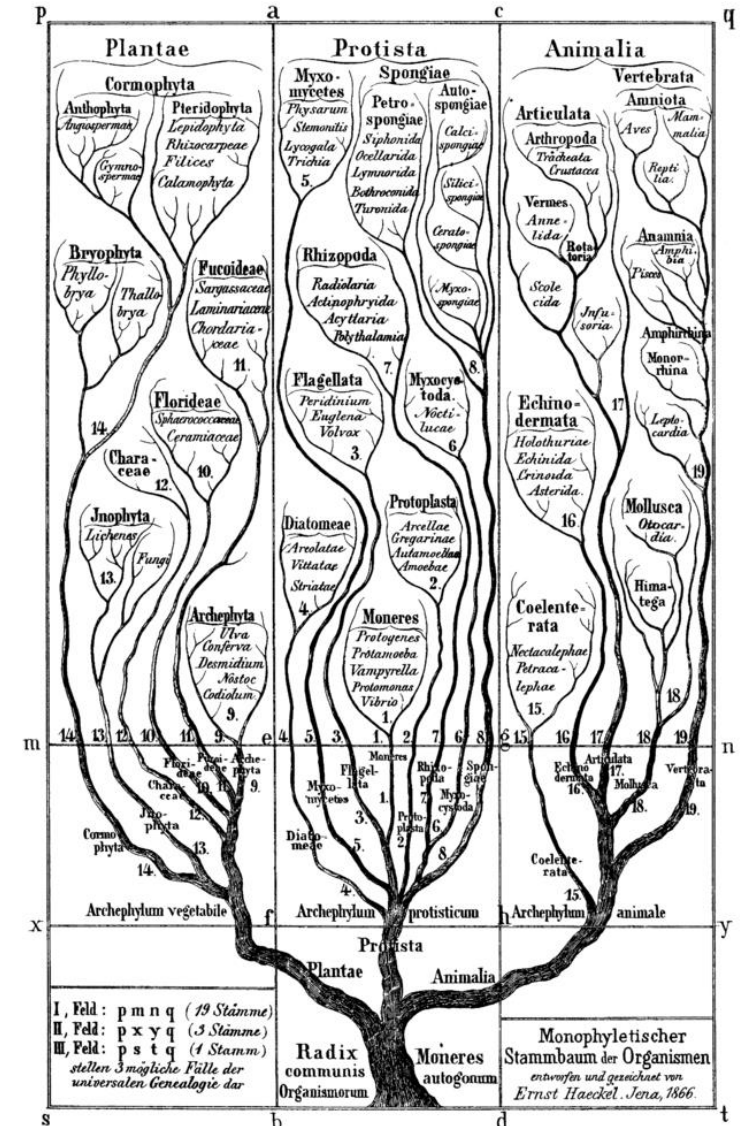


Descent with modification: the meaning of homology

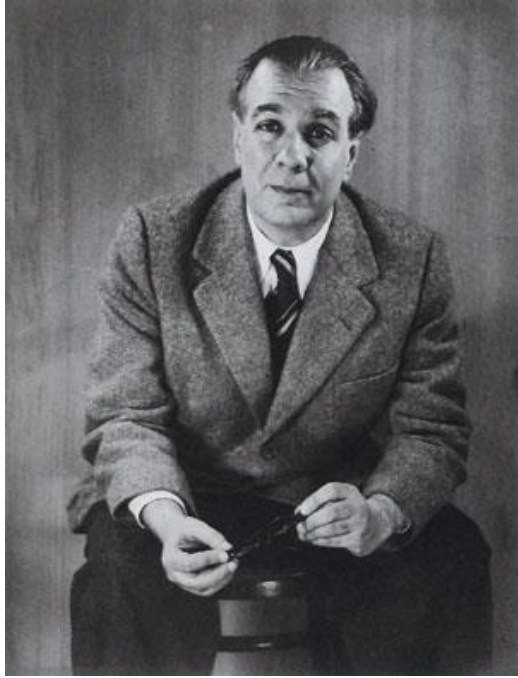


Ernst Haeckel (1834-1919)

The first phylogenetic trees were produced by Haeckel, but due to the absence of a formal method, at the beginning they were mostly speculative (although not always necessarily wrong)



Towards a formalization of evolution: the power of models



Jorge Luis Borges (1899-1986)

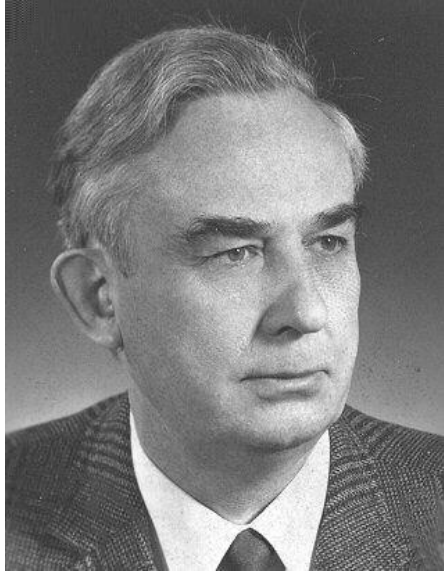
On Exactitude in Science

...In that Empire, the Art of Cartography attained such Perfection that the map of a single Province occupied the entirety of a City, and the map of the Empire, the entirety of a Province. In time, those Unconscionable Maps no longer satisfied, and the Cartographers Guilds struck a Map of the Empire whose size was that of the Empire, and which coincided point for point with it. The following Generations, who were not so fond of the Study of Cartography as their Forebears had been, saw that that vast Map was Useless, and not without some Pitilessness was it, that they delivered it up to the Inclemencies of Sun and Winters. In the Deserts of the West, still today, there are Tattered Ruins of that Map, inhabited by Animals and Beggars; in all the Land there is no other Relic of the Disciplines of Geography.

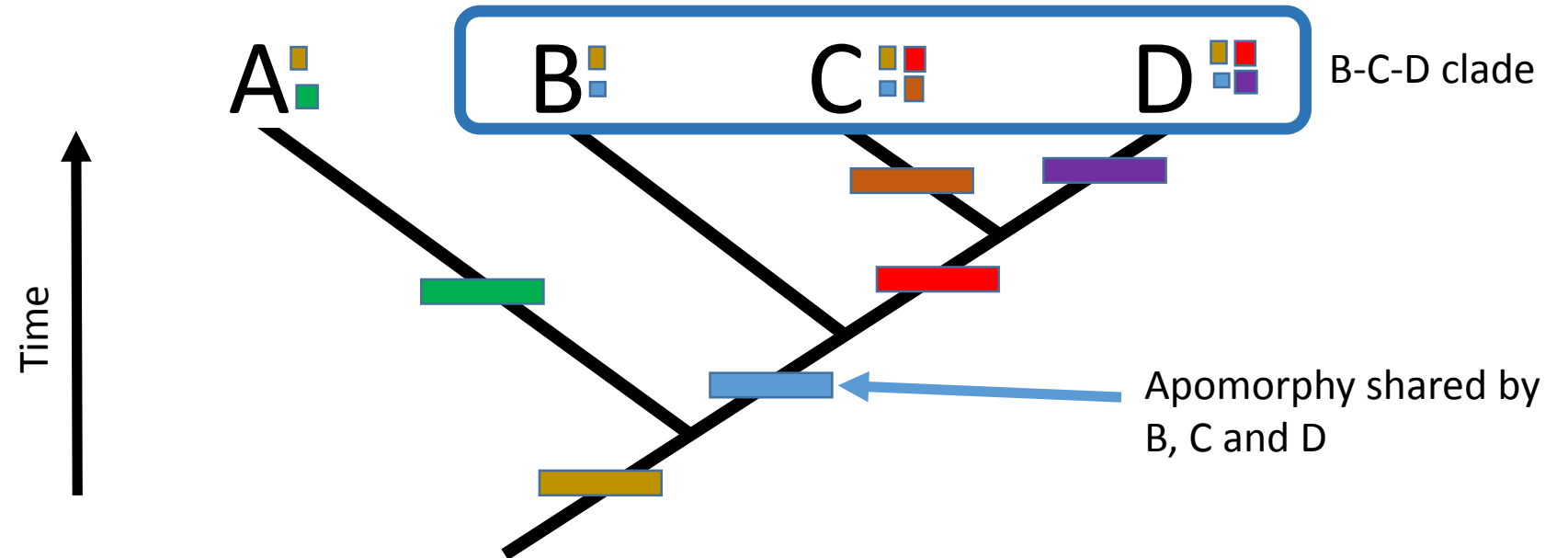
We need models in science in order to handle and interpret data. The “goodness” of a model is often a compromise among accuracy, usefulness to make predictions or plain pragmatism, but remember:

models are never the reality itself

Formalization of evolutionary trees: cladistics



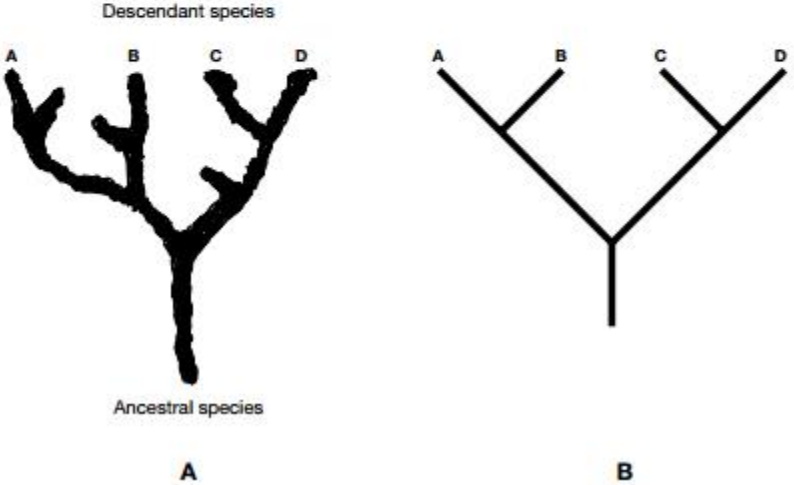
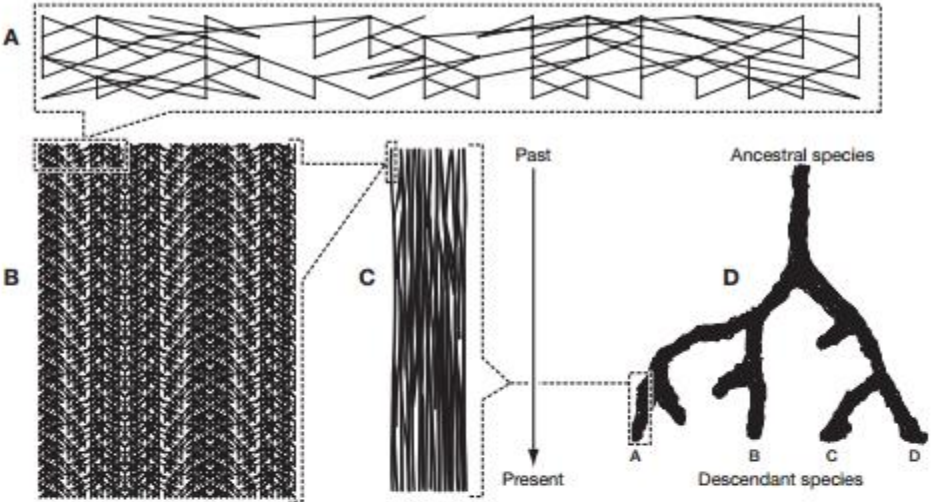
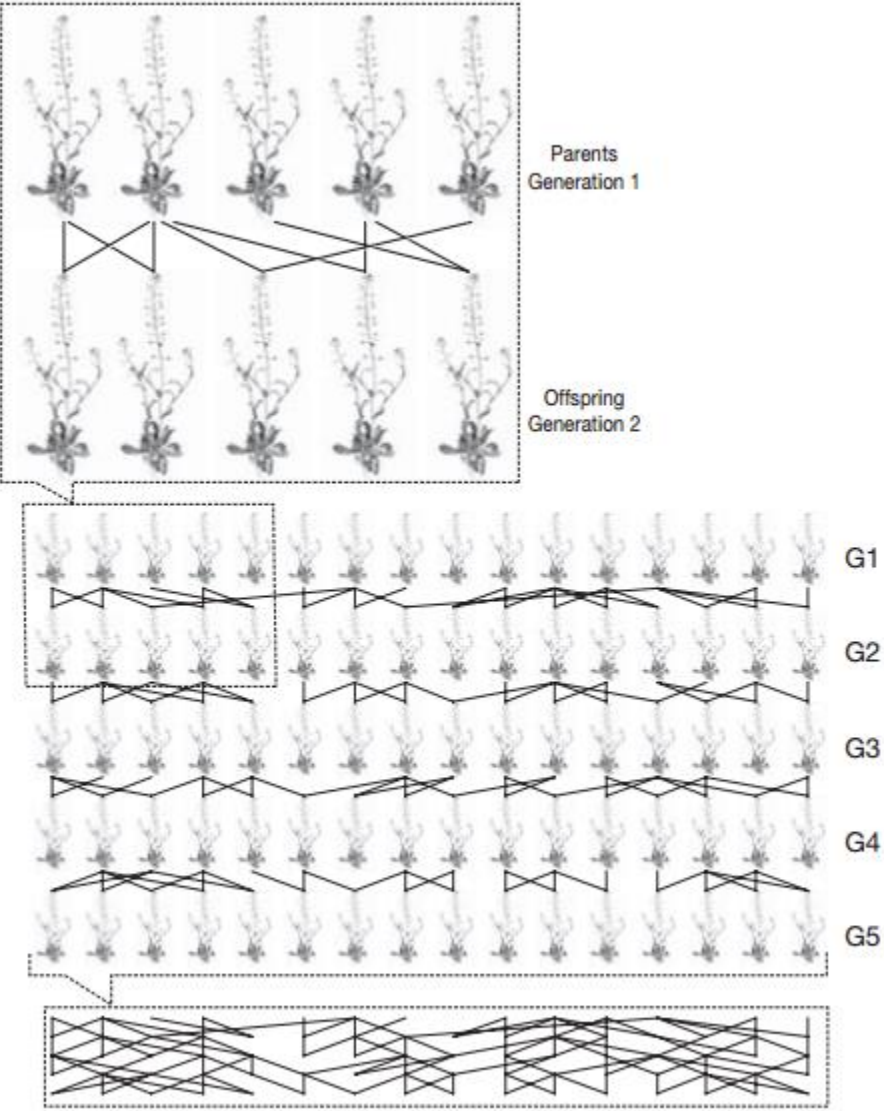
Willi Hennig (1913-1976)



Although often associated to parsimony practice, Hennig's "axioms" are still basic to read a phylogenetic tree:

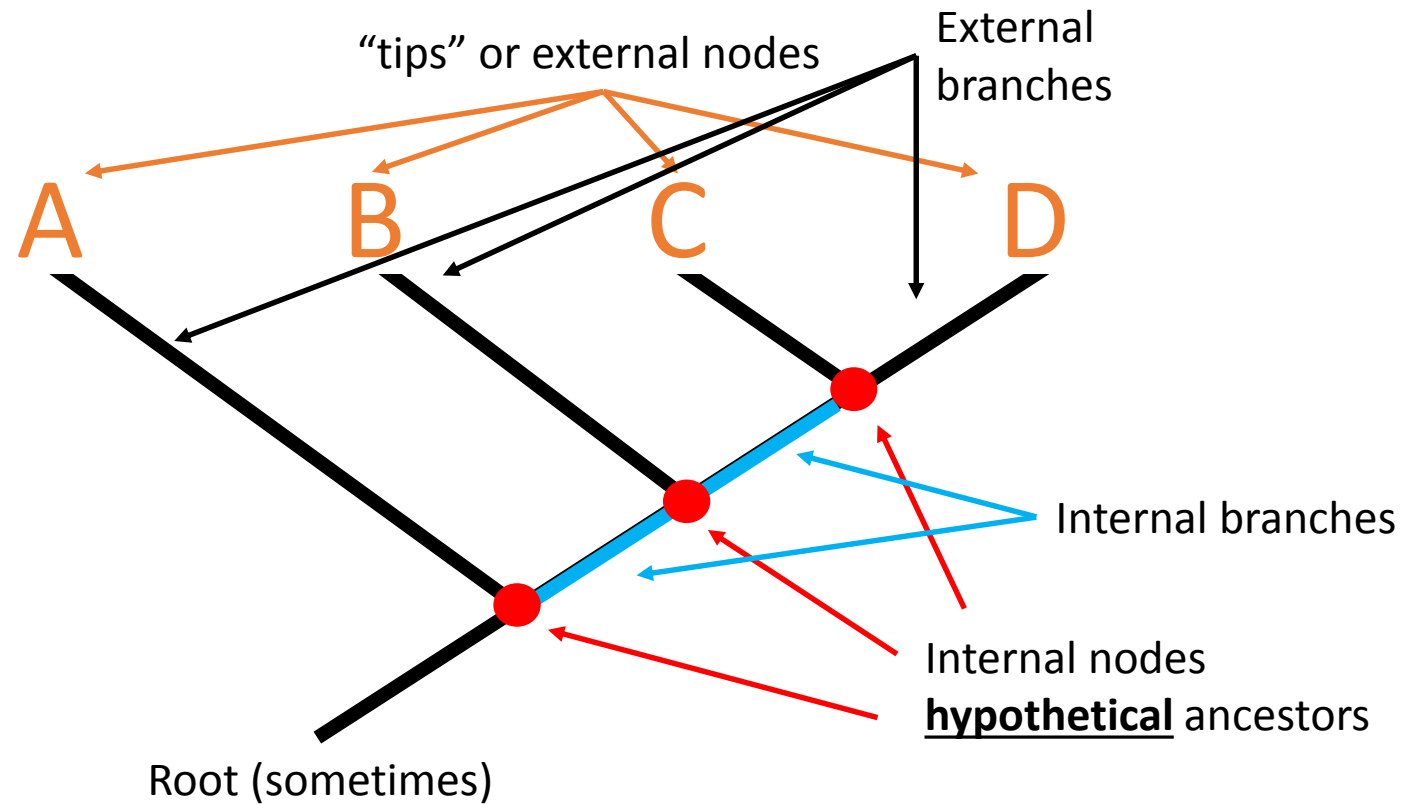
- The relationships among taxa are best represented by hierarchical dichotomous trees
- Only sister-group relationships of the studied taxa can be inferred (ancestral taxa are always hypothetical)
- Homology should be presumed in absence of evidence to the contrary
- Clades (and thus, taxa) are determined by synapomorphies

Formalization of evolutionary trees: cladistics

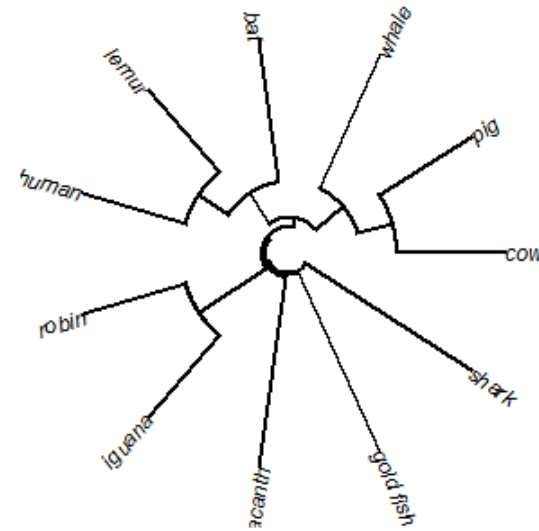
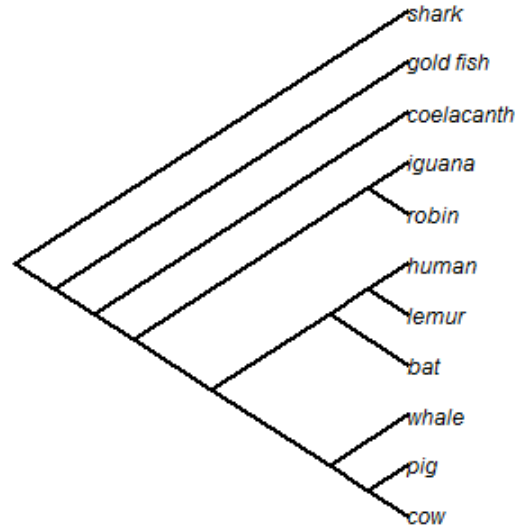
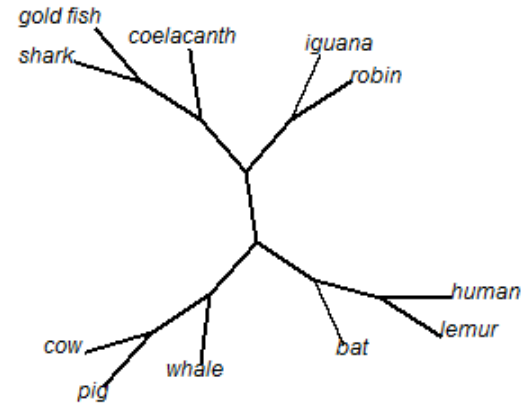
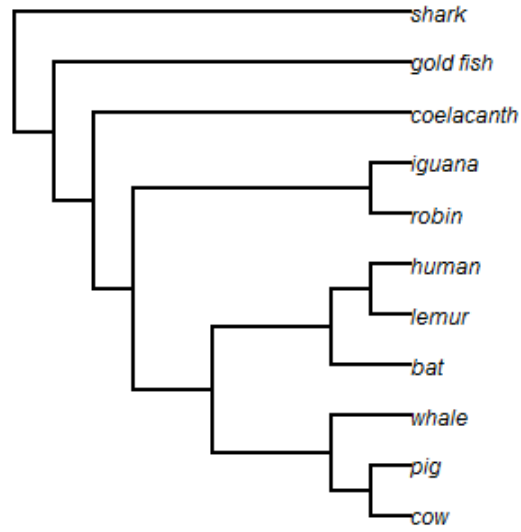


Elements of a tree

A phylogenetic tree is a dichotomous visualization of the sister relationships of a selection of taxa or specimens. Due to its hierarchical structure and its grounds on (presumed) homologous traits, we should understand it as a model of evolutionary history (not as the evolutionary history itself)

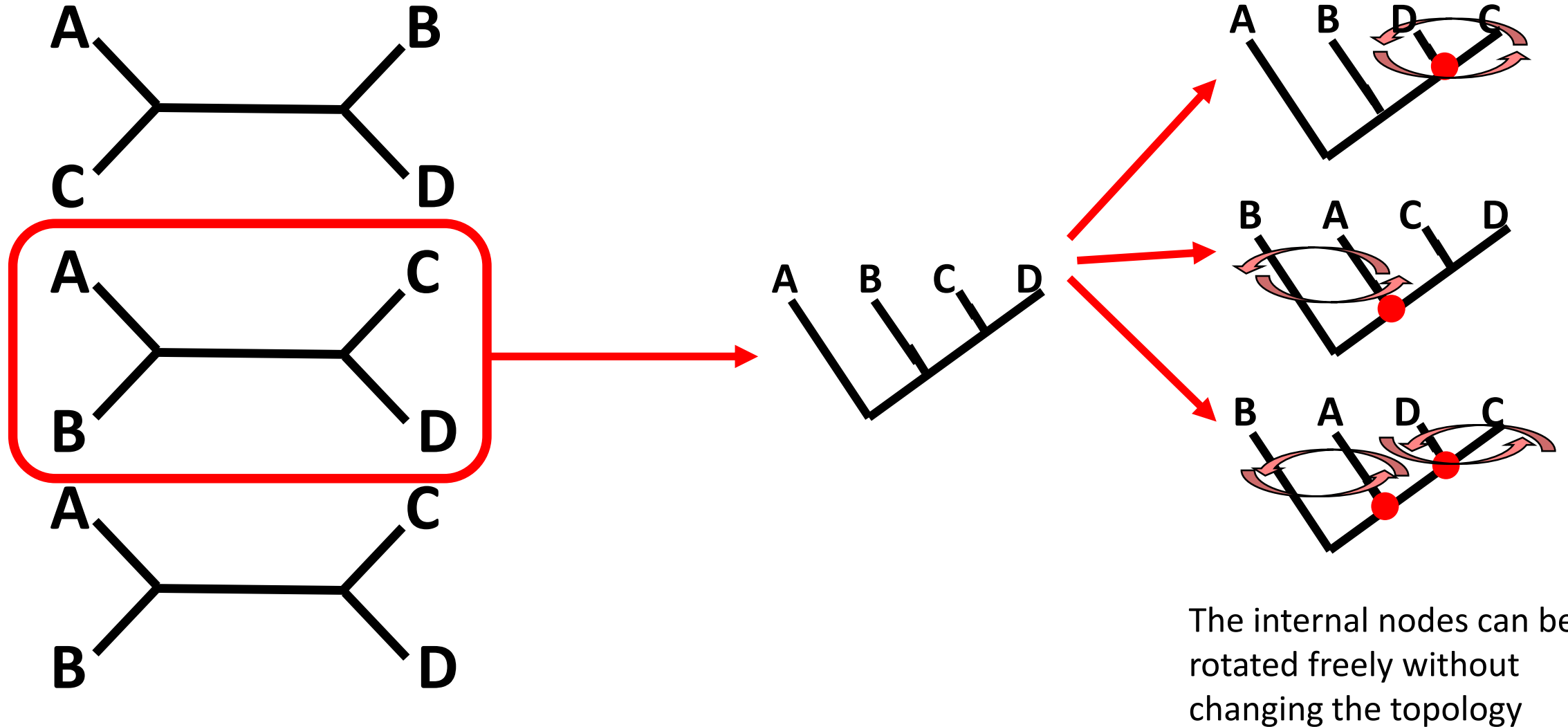


Tree “styles”



Elements of a tree: topology

We call “topology” to the nested relationships of shared common ancestry. Ex: A 4-taxa **unrooted** tree can only have 3 different topologies



Elements of a tree: topology

The number of topologies increase very fast with the number of external nodes

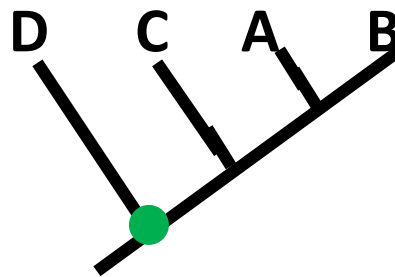
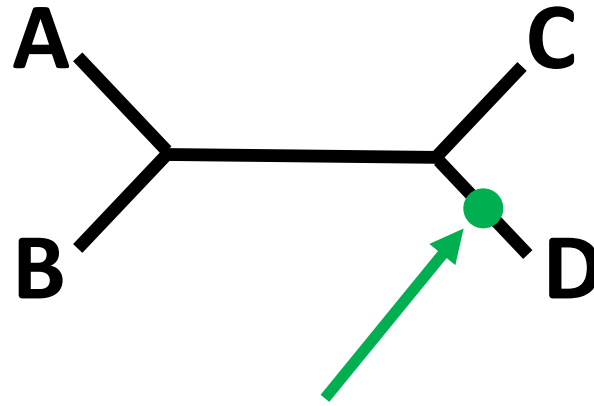
Number of tips	Number of unrooted topologies
1	1
2	1
3	1
4	3
5	15
6	105
7	945
8	10,395
9	135,135
10	2,027,025
20	221,643,095,476,699,771,875
50	3×10^{74}
100	2×10^{182}

Elements of a tree: root

The root is an extra internal node that indicates where the tree “starts”, which is the position of the most basal branch

This information is never included in the dataset, it needs to be added by the researcher (an alignment does not inform explicitly about the flow of evolutionary history)

The most usual way to include a root in an analysis is to add an outgroup (a reference outside of our study group that shares a common ancestor with it)

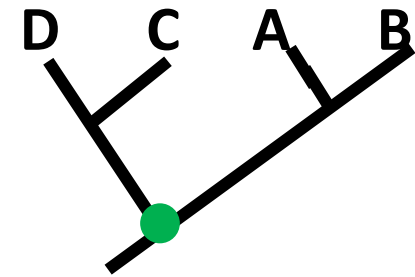
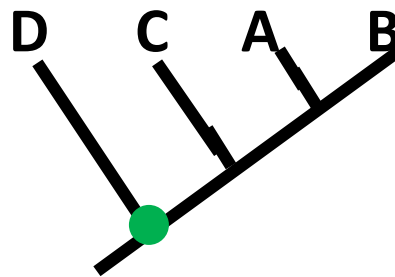
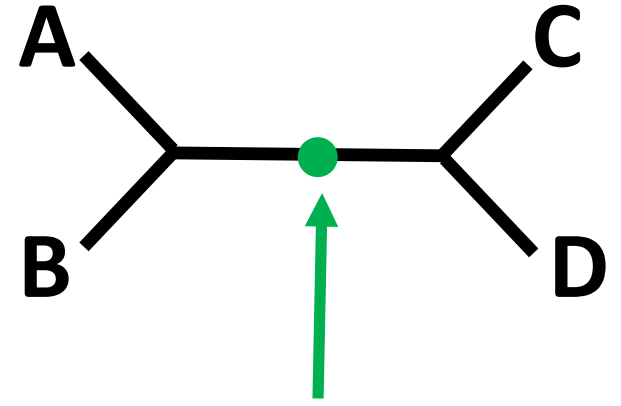
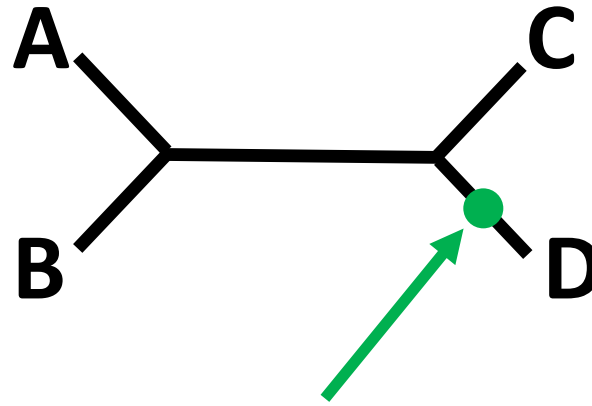


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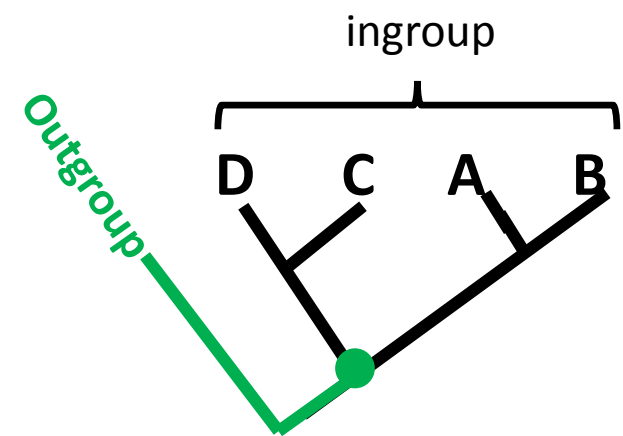
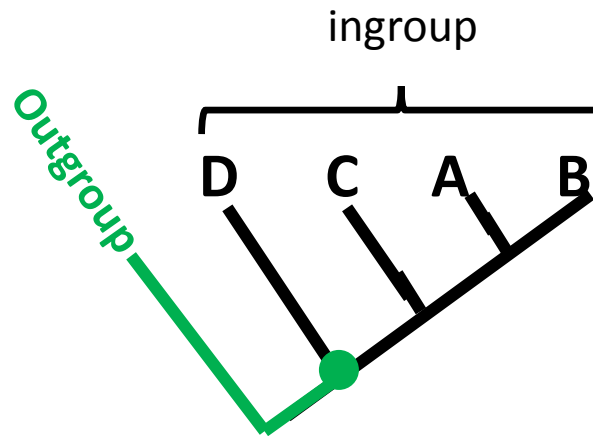
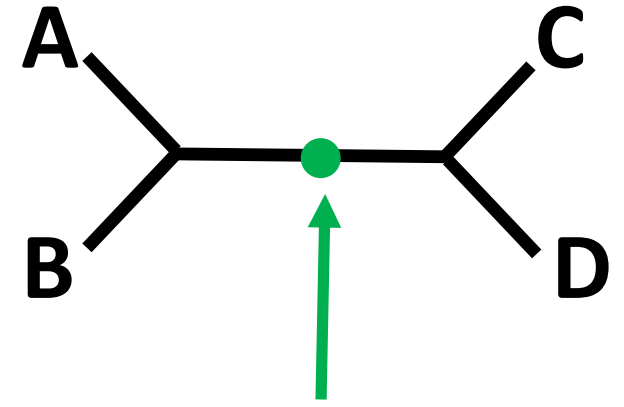
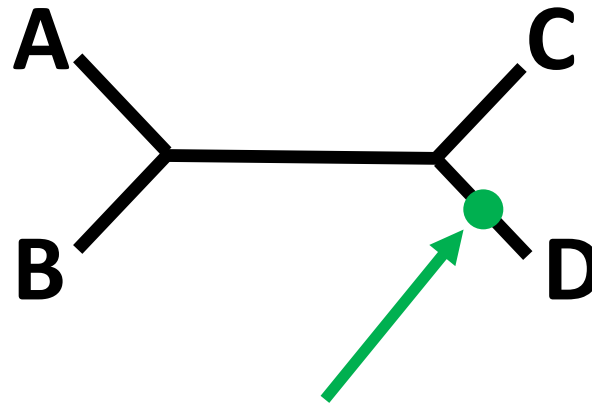


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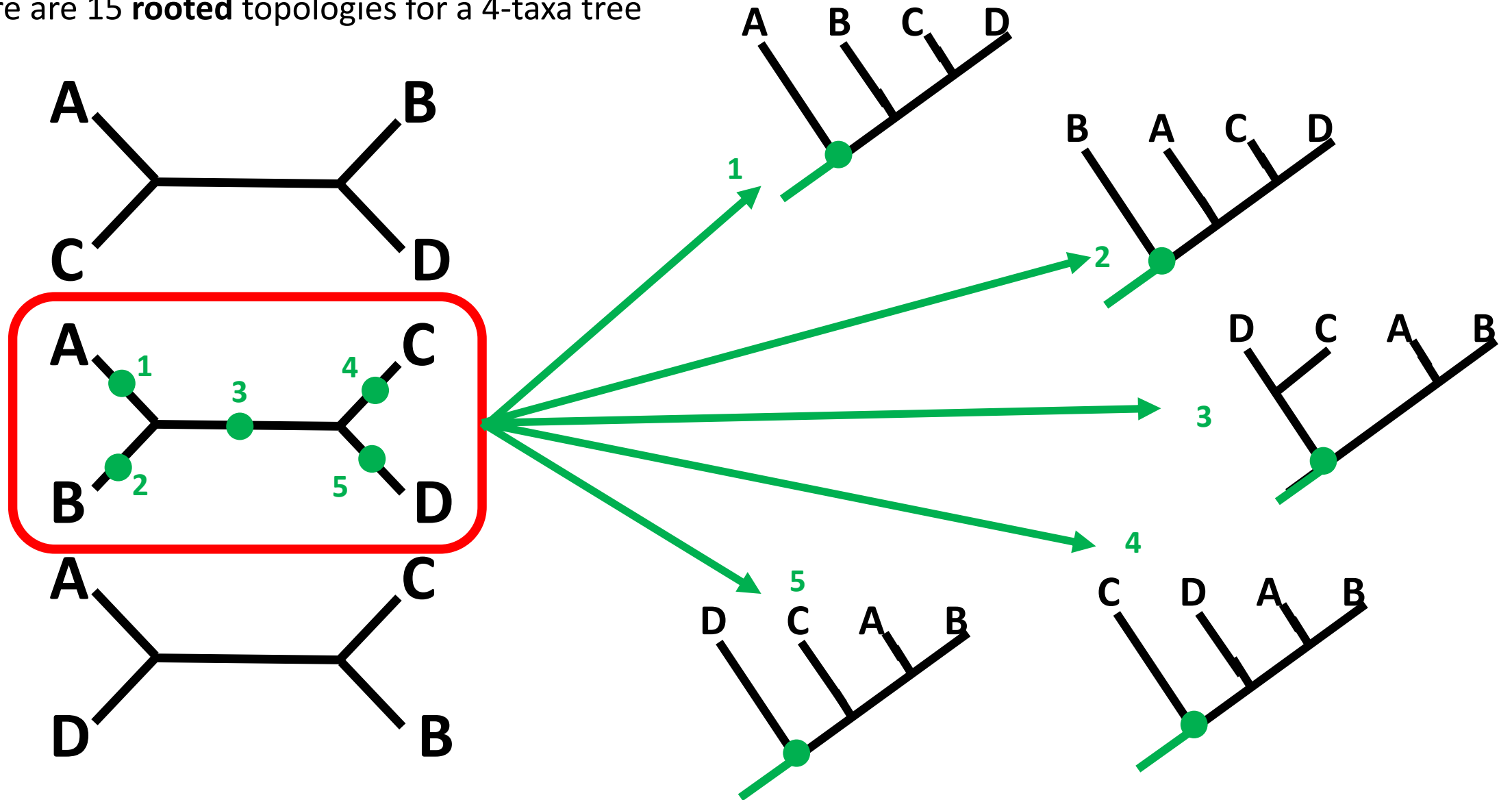
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The most usual way to include a root in an analysis is to add an outgroup (a reference outside of our study group that shares a common ancestor with it)



Elements of a tree: root

There are 15 **rooted** topologies for a 4-taxa tree



Elements of a tree: root

Rooted trees increase their number of topologies at a higher rate than unrooted trees

Number of tips	Number of unrooted topologies	Number of rooted topologies
1	1	1
2	1	1
3	1	3
4	3	15
5	15	105
6	105	945
7	945	10,395
8	10,395	135,135
9	135,135	2,027,025
10	2,027,025	34,459,425
20	221,643,095,476,699,771,875	8×10^{21}
50	3×10^{74}	2.8×10^{76}
100	2×10^{182}	3.3×10^{184}

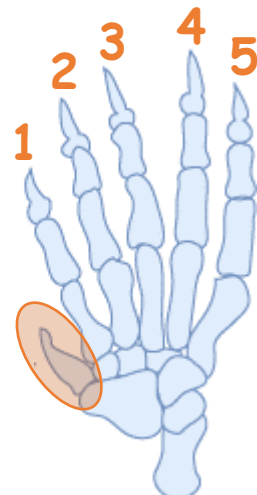
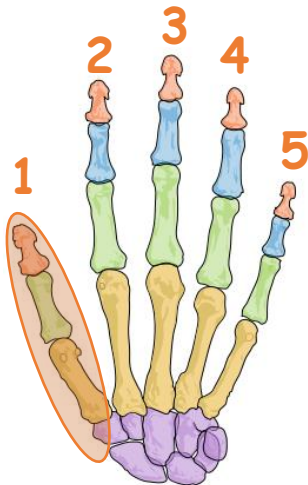
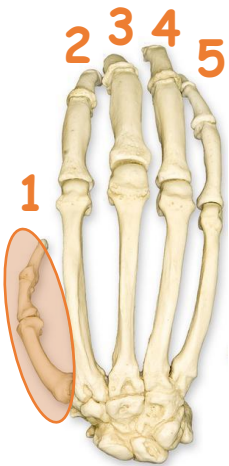
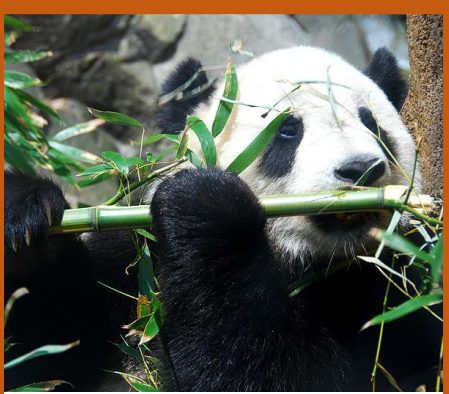
Elements of a tree: characters

mammals with opposable “thumbs”



Does this character qualify them to be sorted in the same taxon?

Elements of a tree: charactes



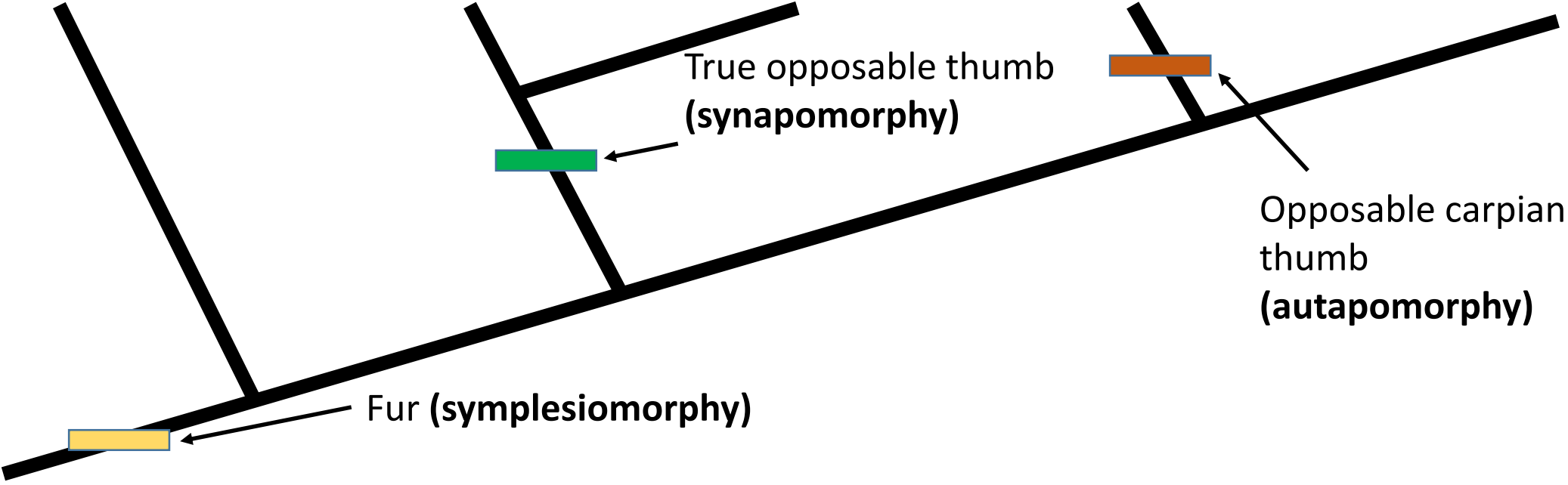
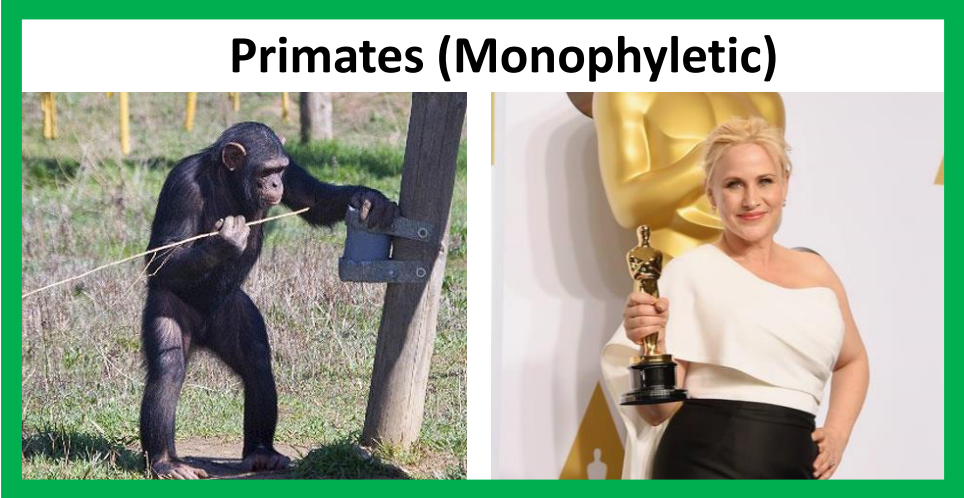
Homology



Homoplasy

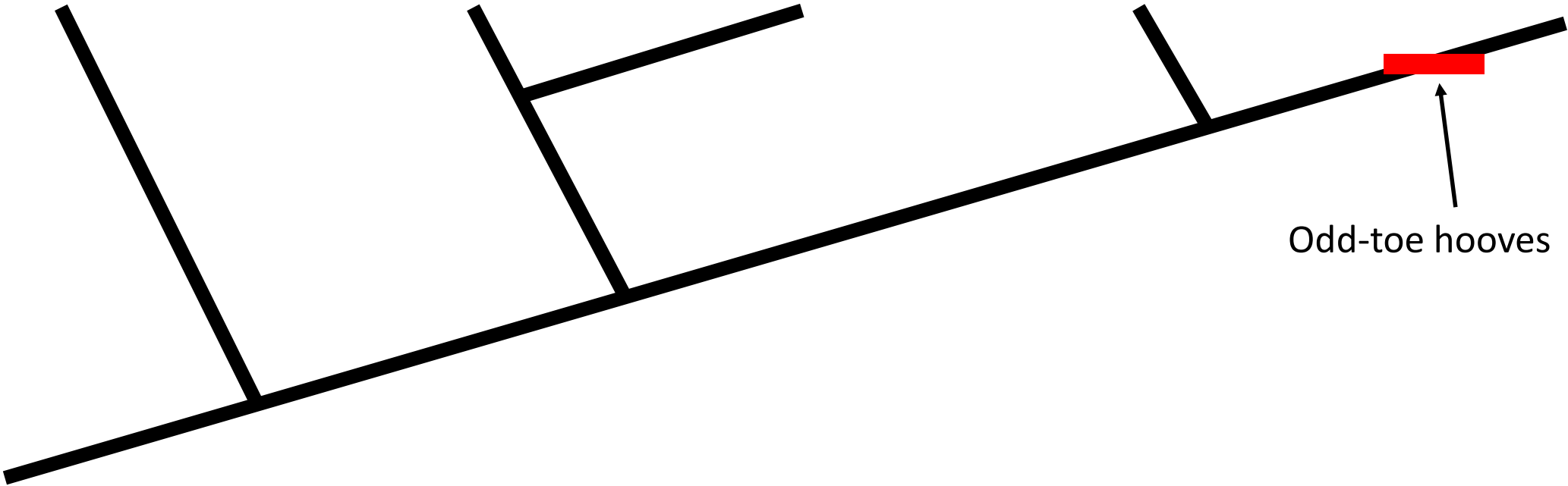


Elements of a tree: characters



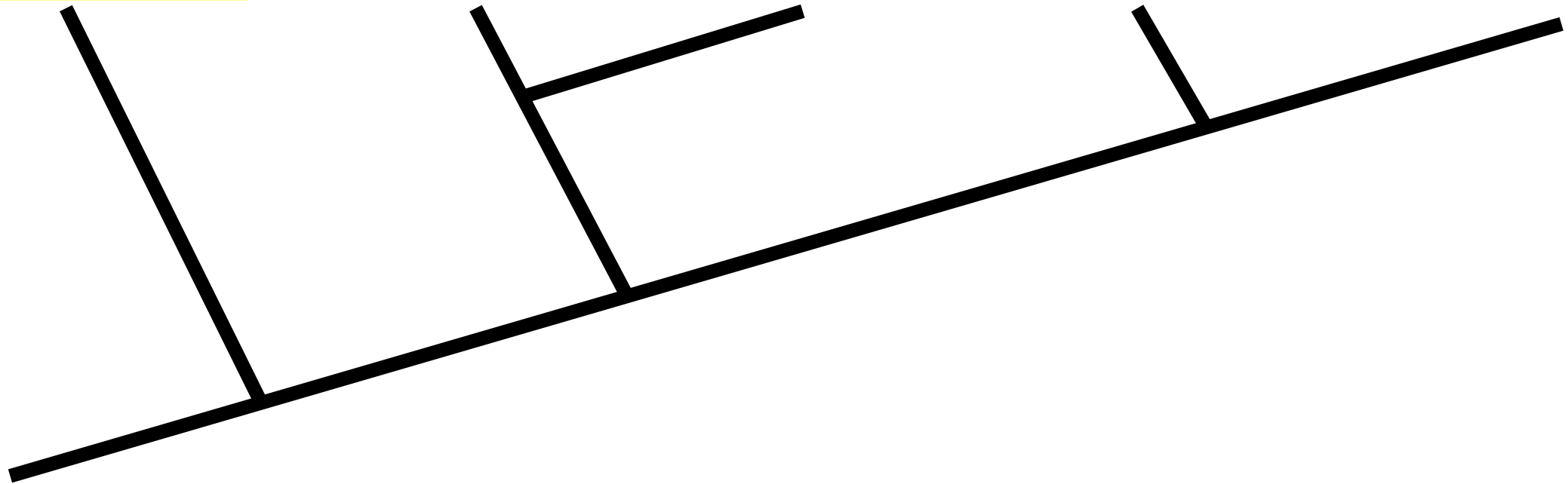
Elements of a tree: characters

Mammals without odd-toe hooves (Paraphyletic, or “grade”)



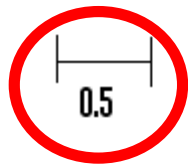
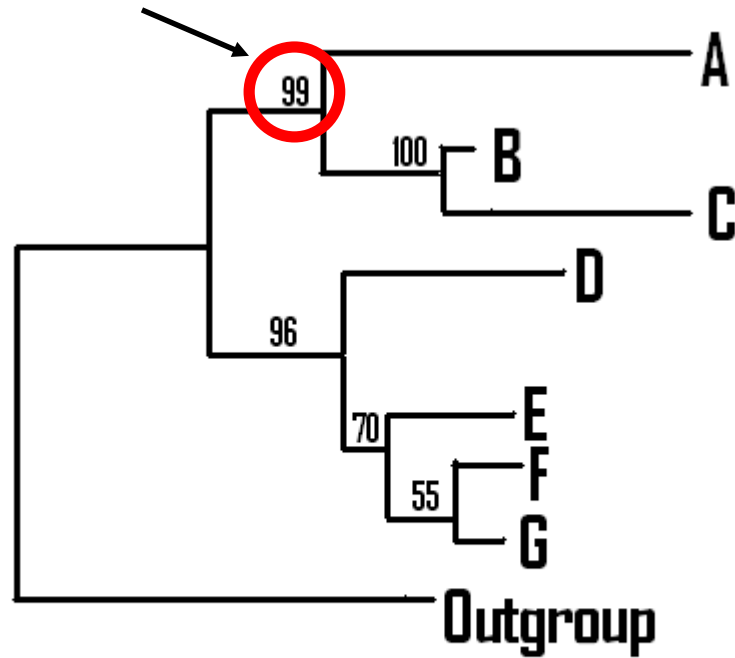
Elements of a tree: characters

Living in temperate areas of the World (polyphyletic, non phylogenetically informative assemblage)

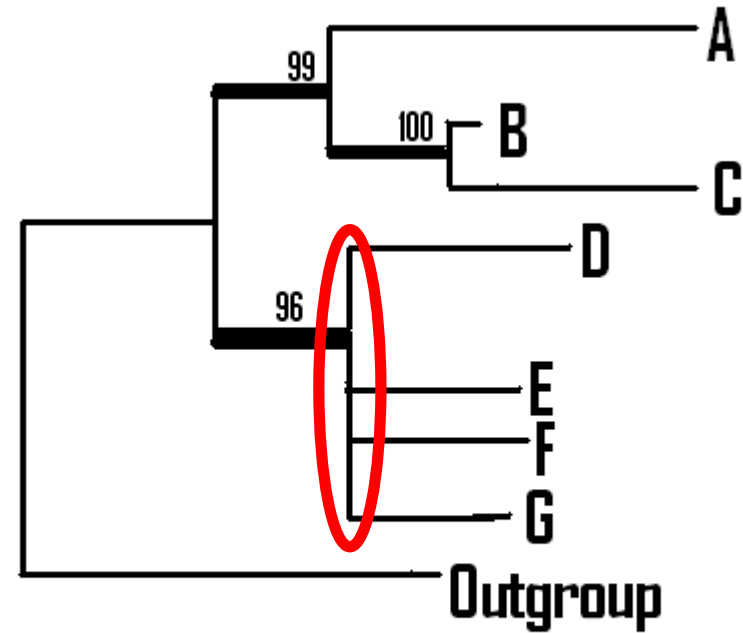


Elements of a tree: scales and support values

Support value of an internal branch. Given in percentages (0-100) or probability (0-1)



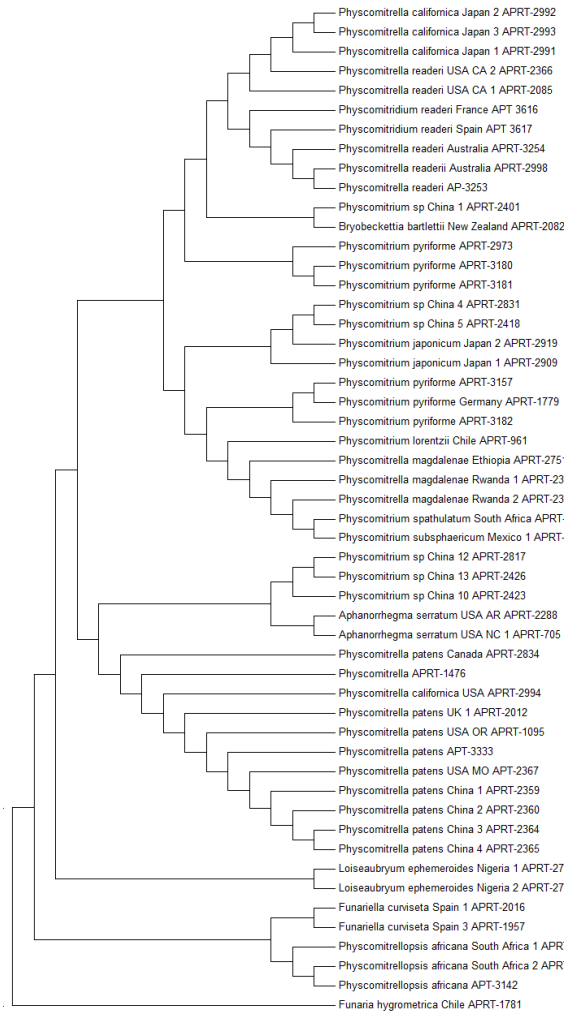
Scale of branch length. Number of changes in a branch (e.g.: number of substitutions per site)



When the support of some internal branches is too low, typically they are collapsed on a polytomy (unresolved node)

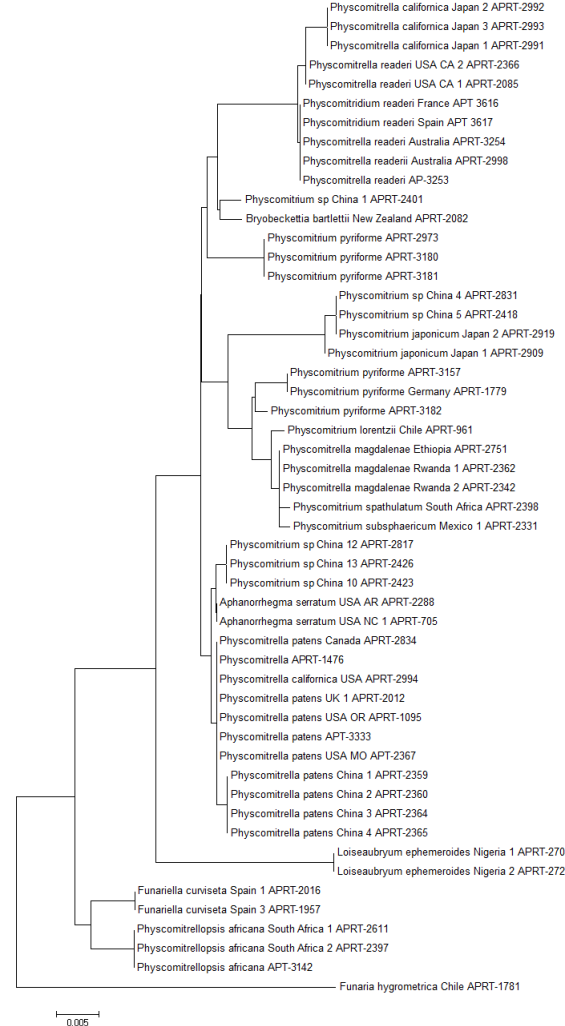
Types of trees

Cladogram



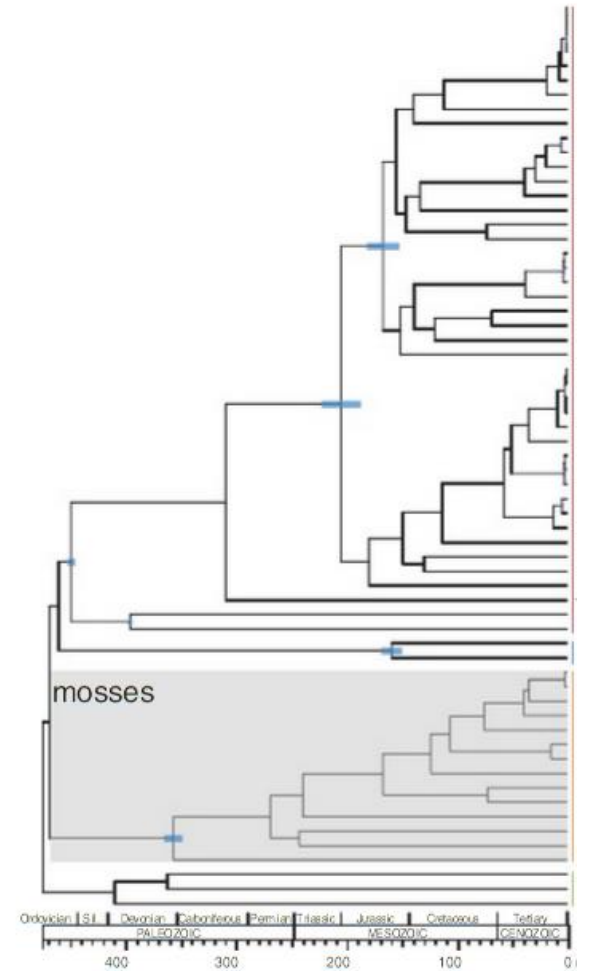
Shows only topological relationships

Phylogram



Topological relationships and branch lengths

Chronogram



Topology on a time scale

Liu et al. 2015

Phylogeny: what can we learn



Phylogeny: what can we learn

Hypothesis 1



Ugly



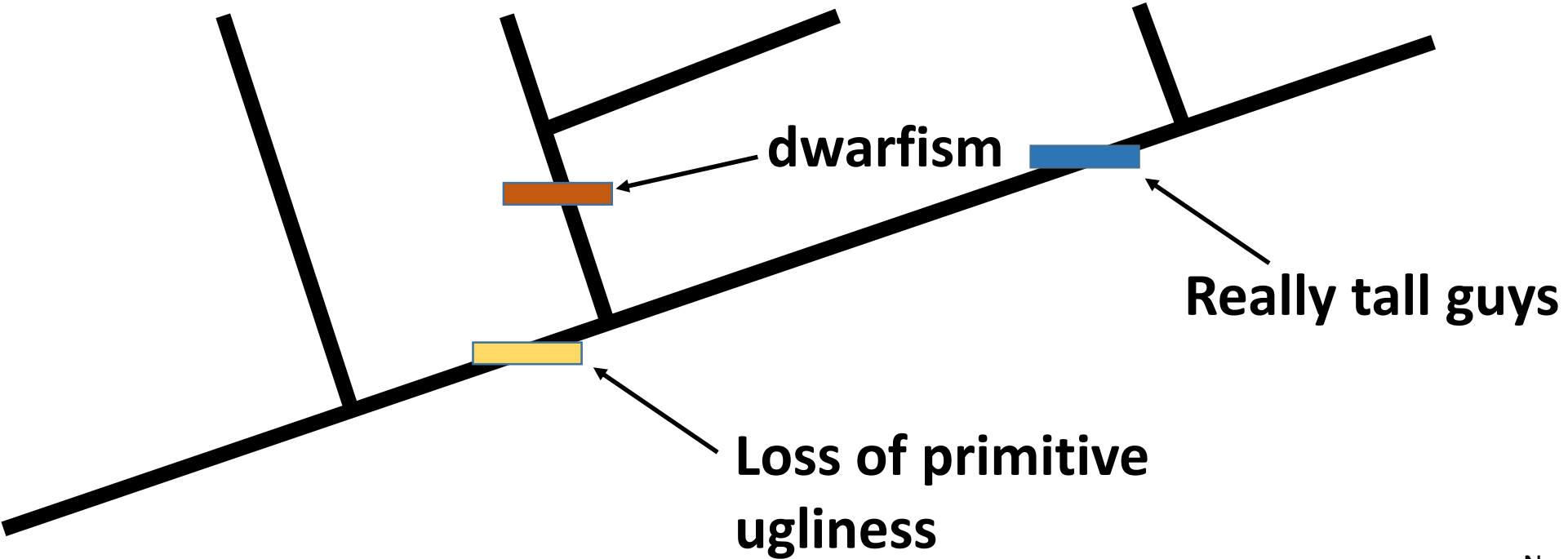
Short



Tall

Phylogeny: what can we learn

Hypothesis 1



Phylogeny: what can we learn

Hypothesis 2



Ugly



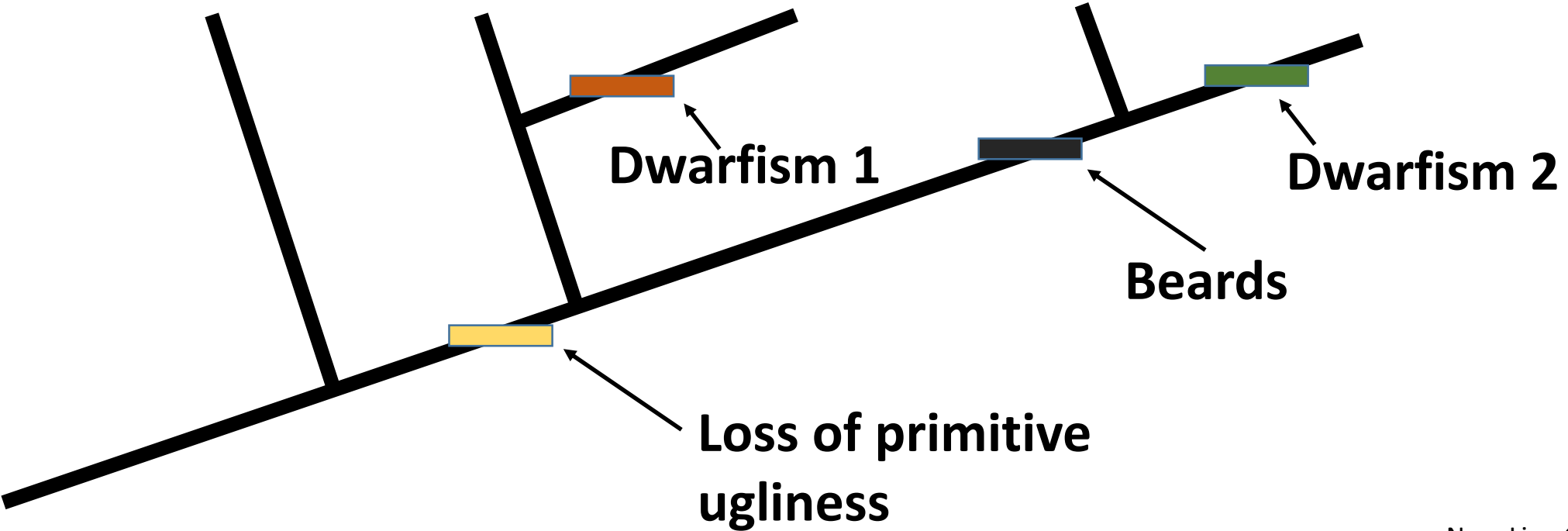
Smooth-faced



Bearded

Phylogeny: what can we learn

Hypothesis 2



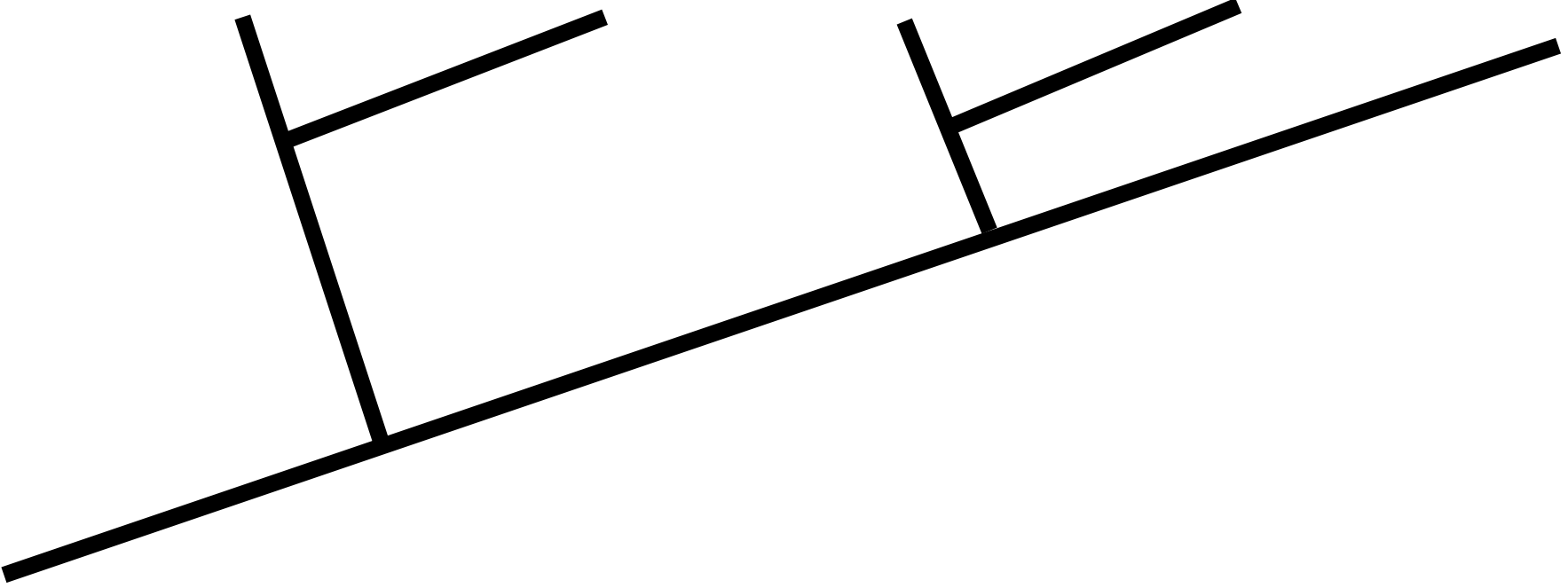
Phylogeny: what can we learn

But... what if we really check the real history (as told by Tolkien himself)



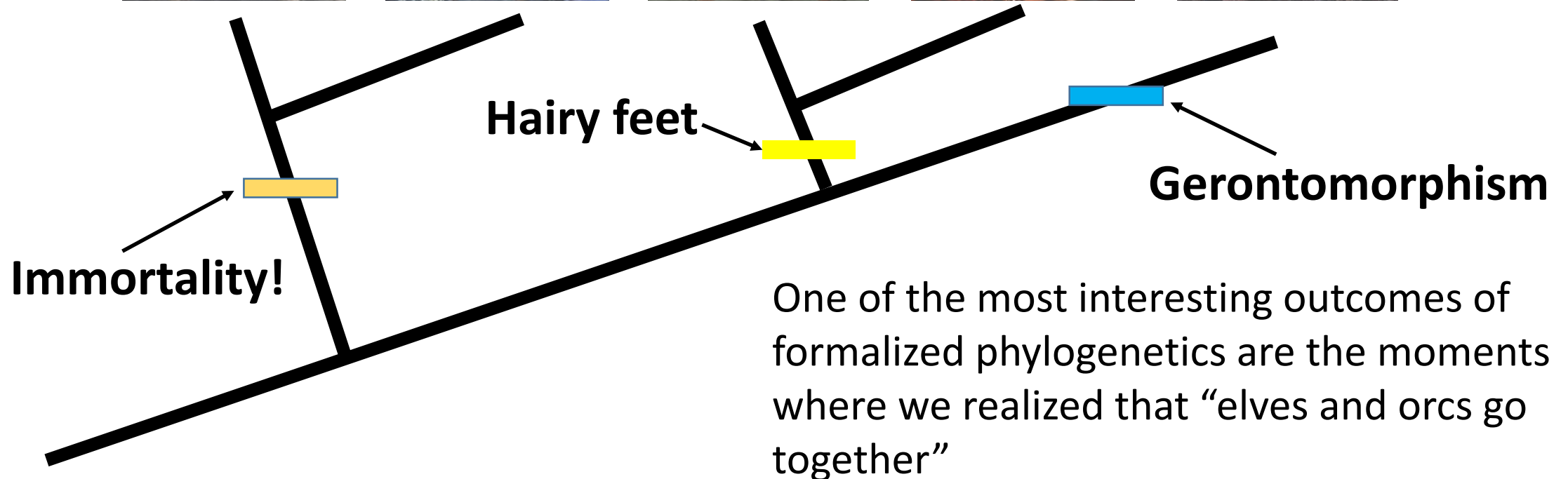
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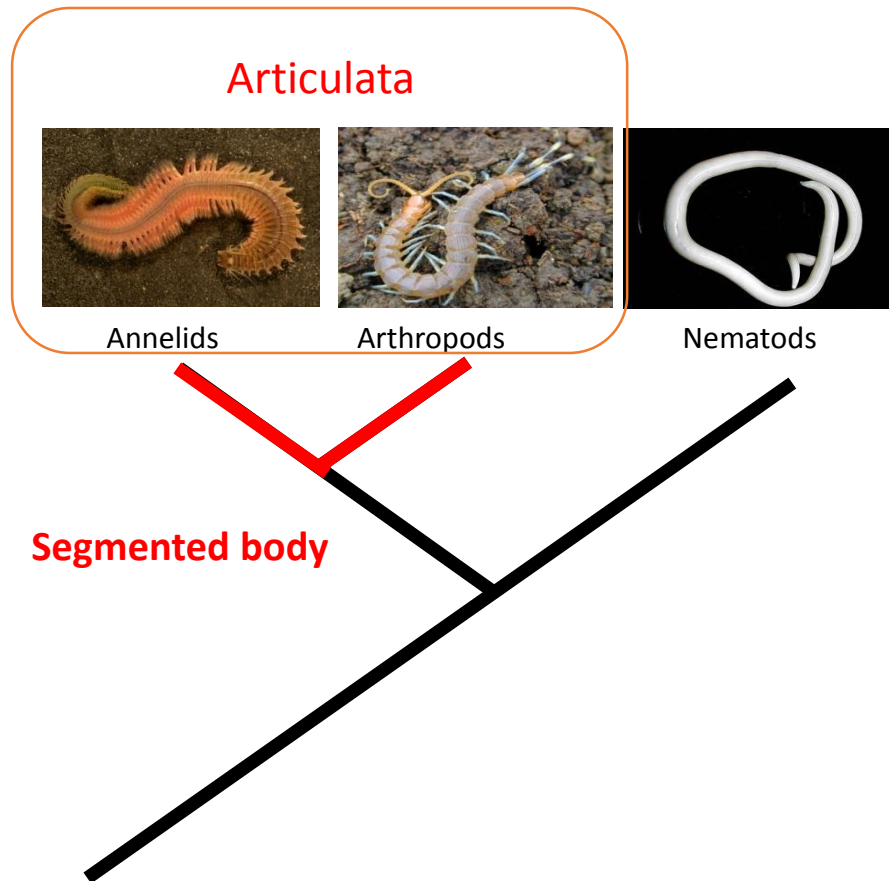
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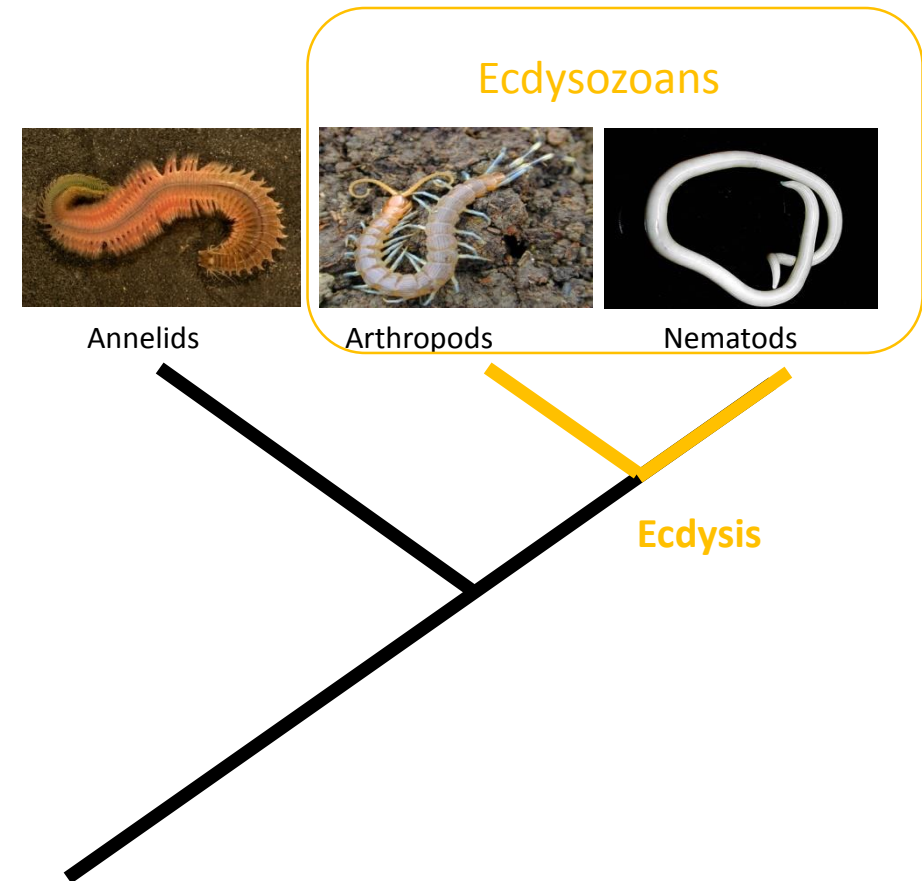


“Orcs and elves”

Traditional hypothesis



Ecdysozoan hypothesis



“Orcs and elves”



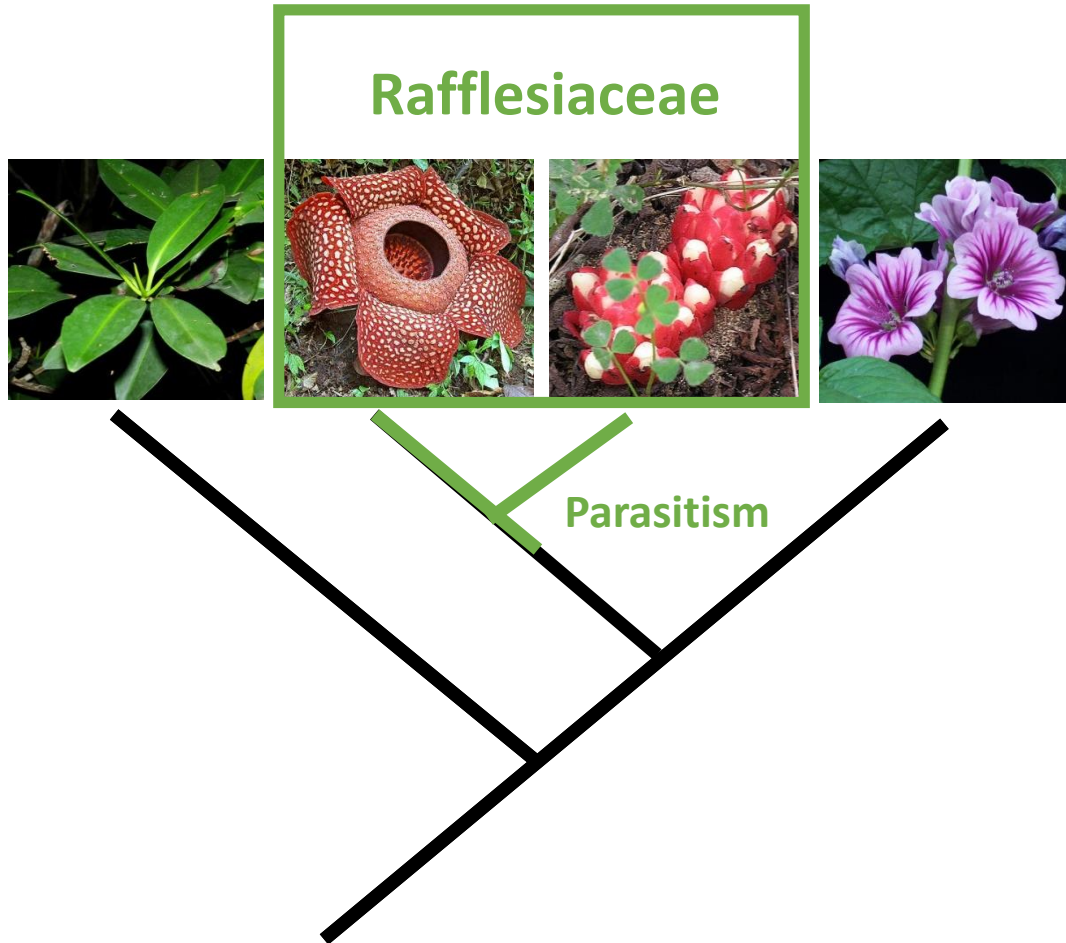
Rafflesia arnoldii



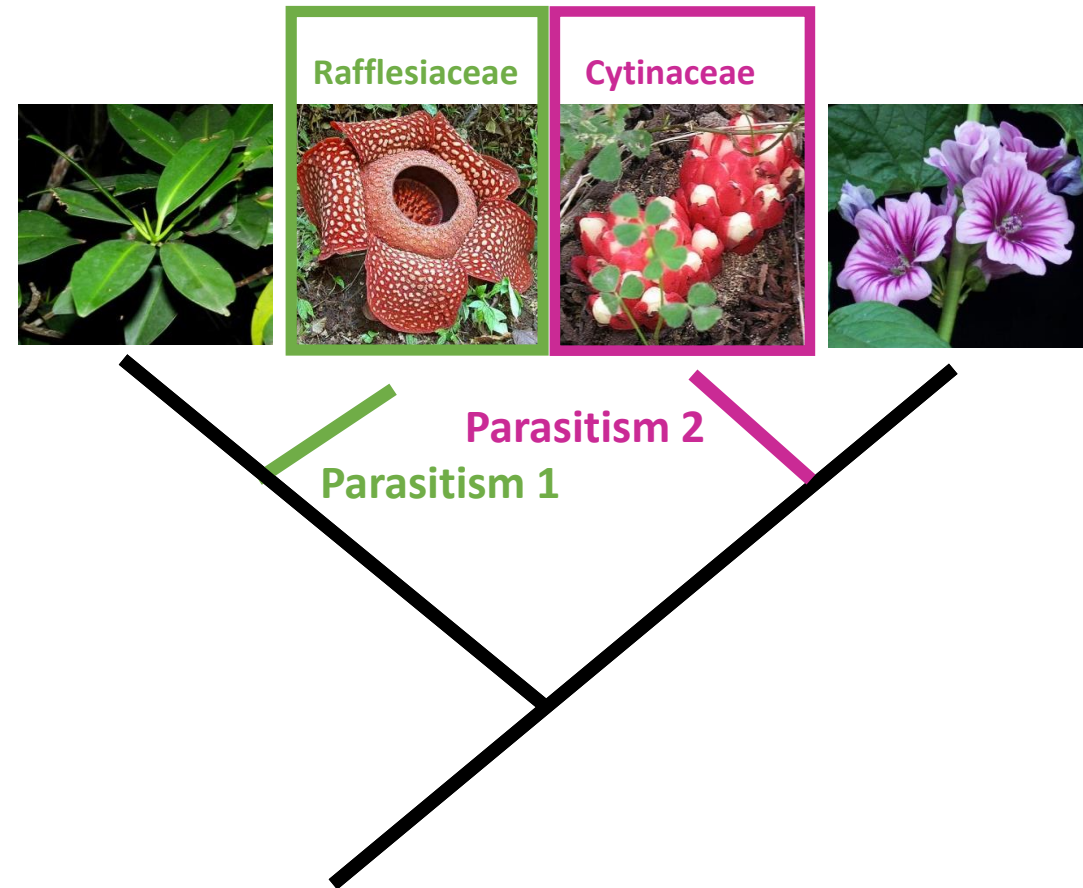
Cytinus hypocistis

“Orcs and elves”

Traditional hypothesis



After Angiosperm Phylogeny Group



“Orcs and elves”



Buxbaumia (Bug moss), saprophytic

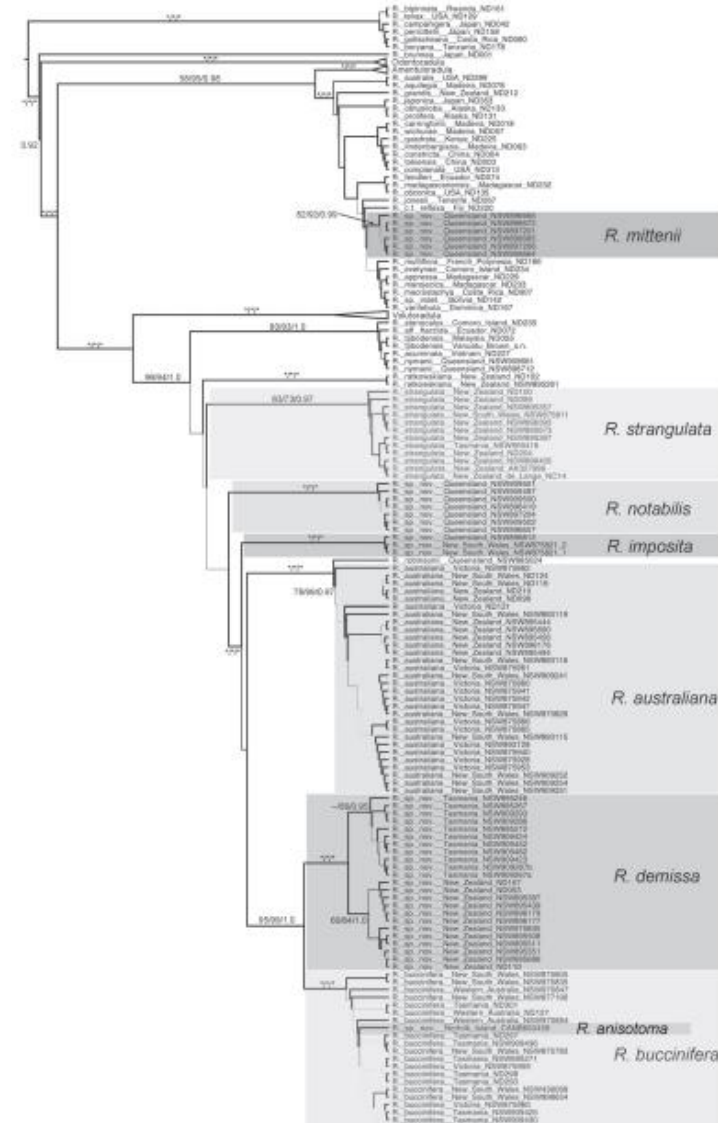
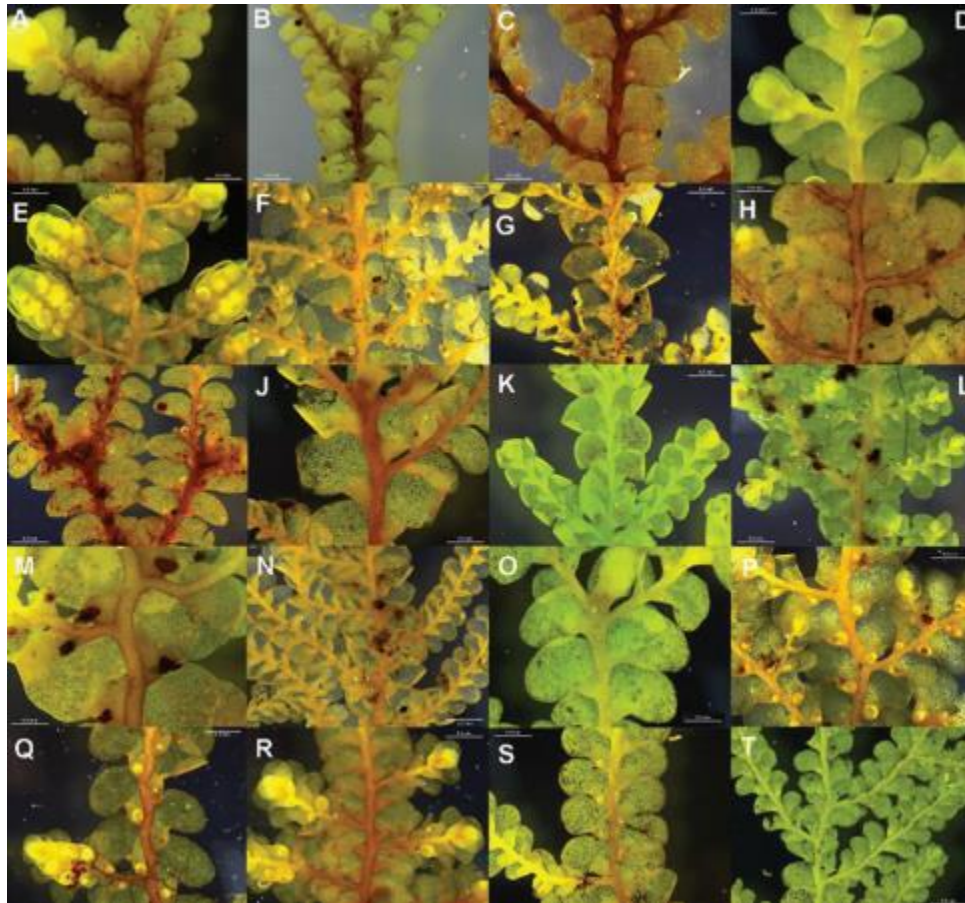


Polytrichum (hair moss), has water conducting tissue, which is homoplasious to vascular tissue in higher plants

Both are basal mosses, but were traditionally treated as derived lineages in moss phylogeny

Interest of phylogeny: improving taxonomic resolution

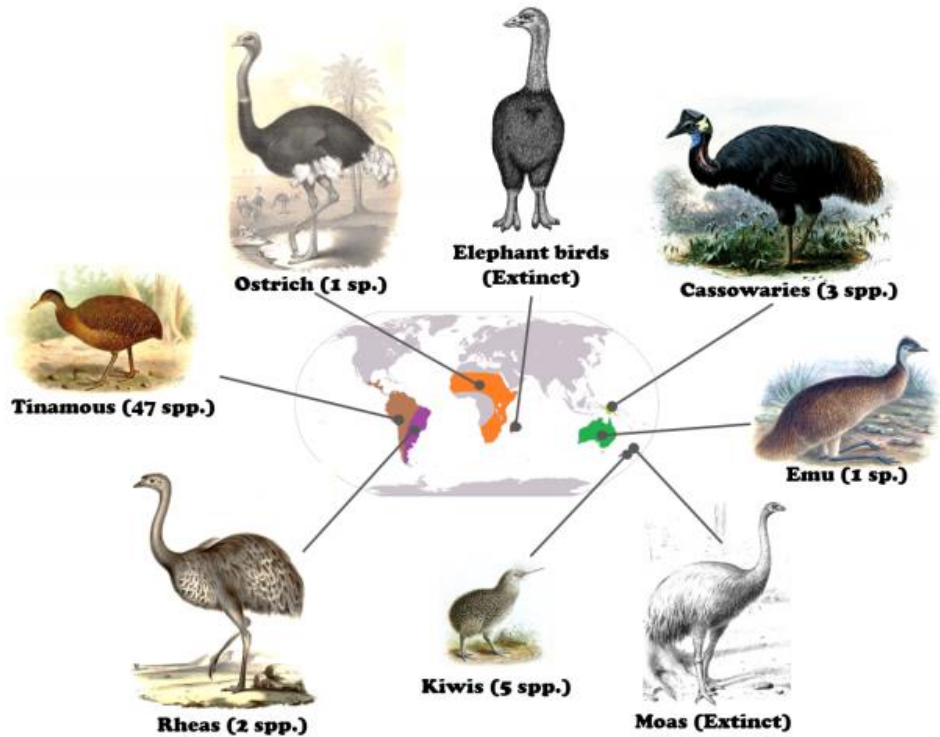
Discovering cryptic species of Australasian liverworts



Renner et al. 2013. Phytokeys 27: 1-113

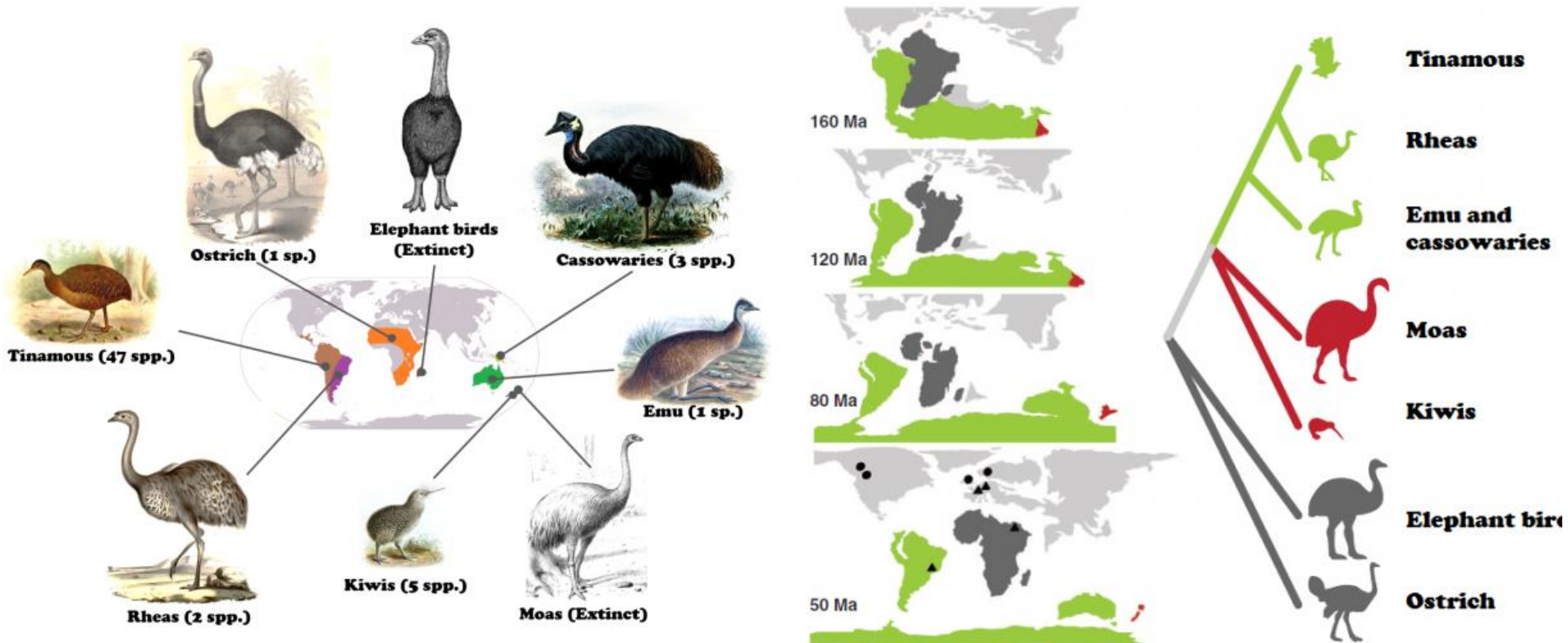
Interest of phylogeny: unraveling relationships

Ratites biogeography



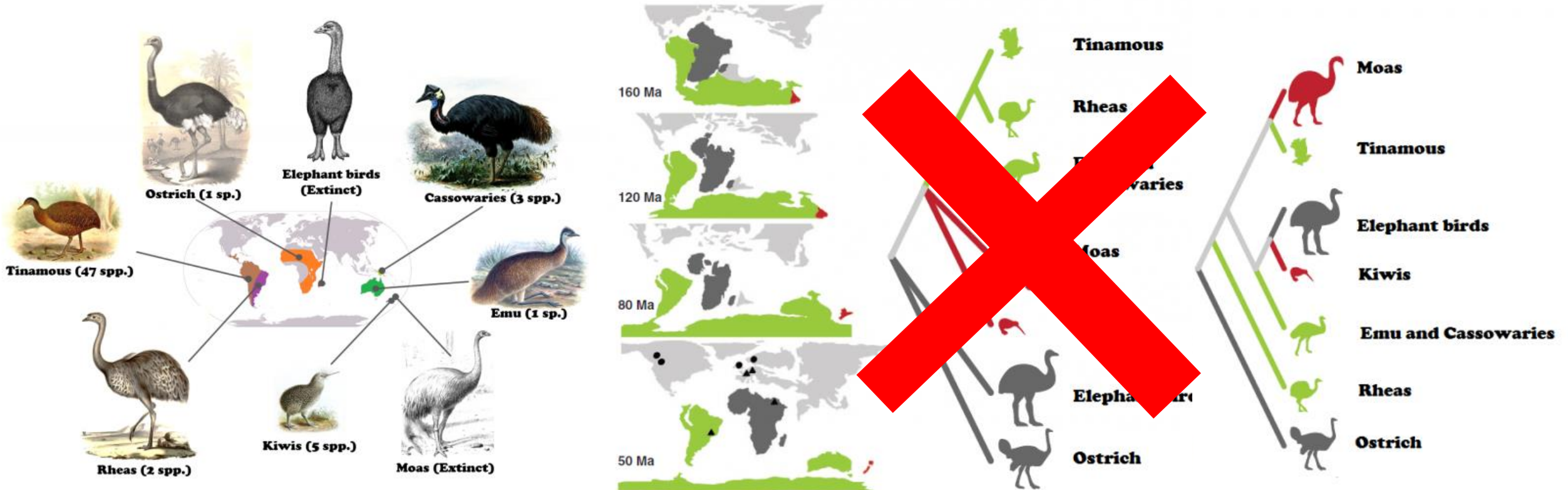
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Interest of phylogeny: unraveling relationships

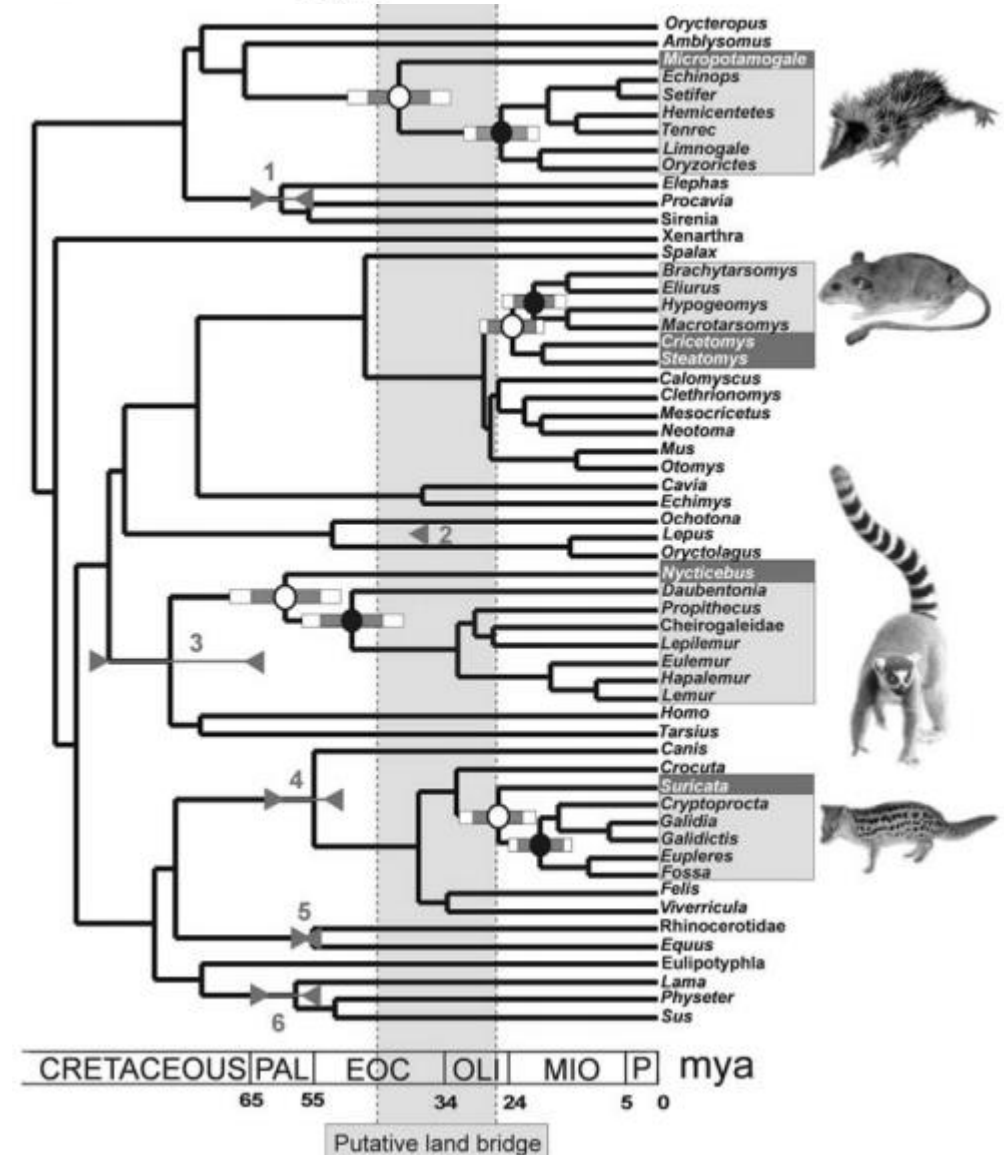
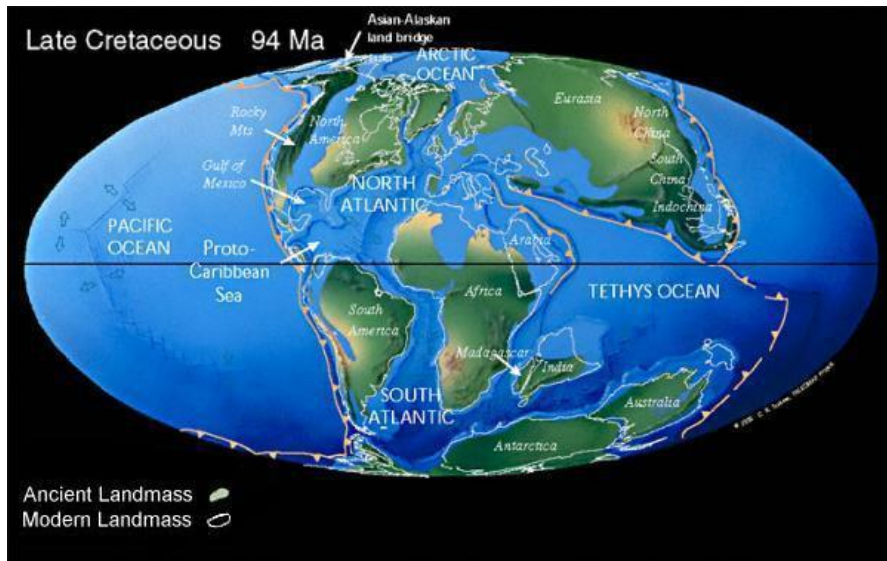
Ratites biogeography



Mitchell K.J., et al. (2014). Science, 344 (6186)

Interest of phylogeny: timing evolutionary events

Mammal colonization of Madagascar



Poux et al. 2005. Systematic Biology 54: 719-730

Interest of phylogeny: epidemiology

Resolution of criminal HIV transmission case

