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1st GYPSUM ECOSYSTEM RESEARCH CONFERENCE

June 3-9, 2018 Ankara/Turkey - Gypsum Ecosystems as biodiversity hotspots

Registration Deadline is May 15th 2018.>



GYPWORLD

A GLOBAL INICIATIVE TO UNDERSTAND GYPSUM ECOSYSTEM ECOLOGY



GYPWORLD Training Course

Analysis of Phylogenies

Part 1: Phylogenetic study design: How to sample appropriate study units

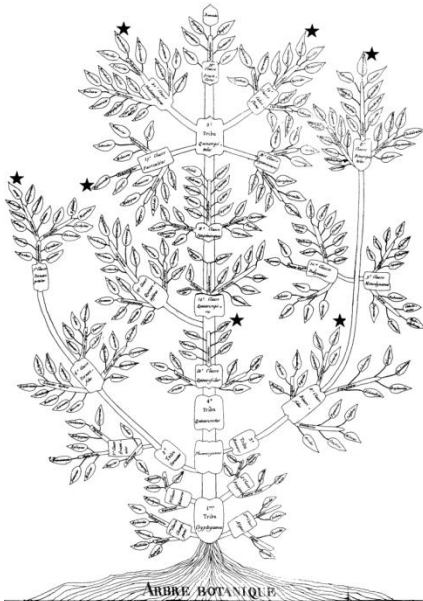


Helga Ochoterena

Introduction: evolution vs phylogeny

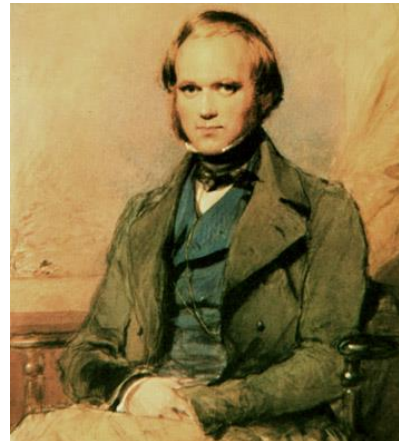
Darwin suggested in 1859 that all living organisms are connected through evolution, sharing a single common ancestor (**descent with modification**).

Even though the notion of modification through time (evolution) was present before, Darwin's contribution revolutionize science, since he suggested a mechanism to explain evolution
(**adaptation and natural selection**).

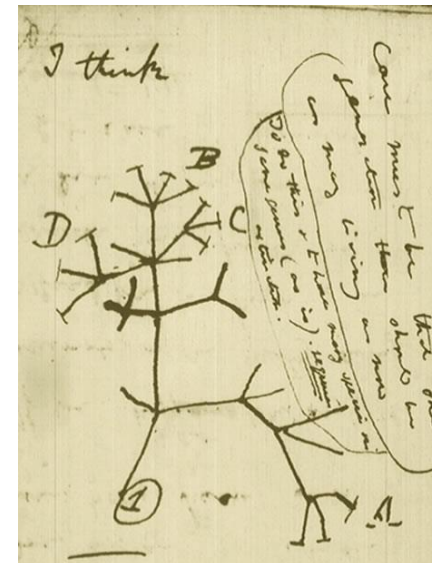


Augustin Augier 1801

<http://listoffigures.wordpress.com/tag/augustin-augier/>



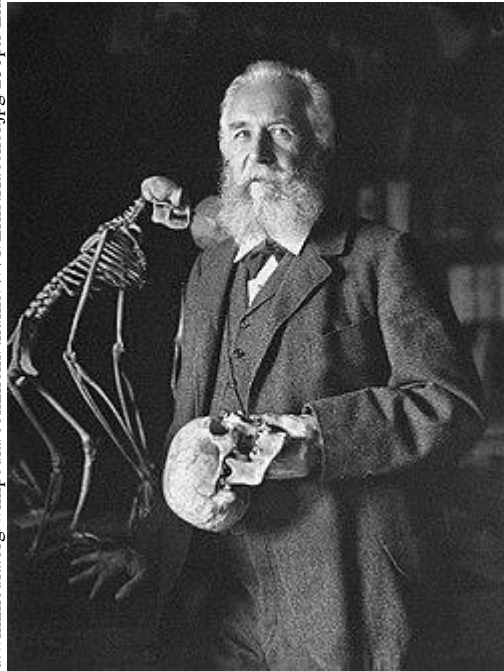
http://www.charlesdarwin.fr/dico_esp.html



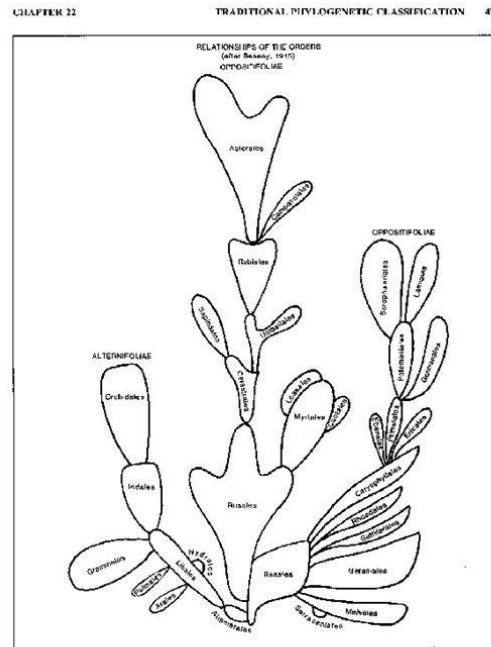
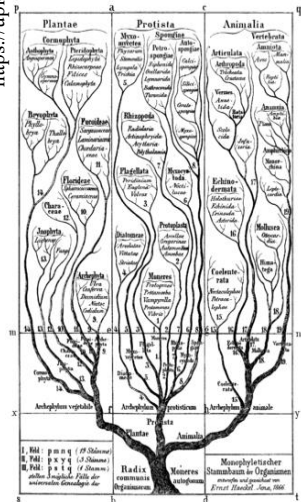
<http://cmcdianatausia.blogspot.mx/2012.html>

Introduction: evolution & phylogeny

Since that moment, questions related to evolution (e.g., how to establish evolutionary hypotheses, major adaptive changes, “trends”, etc.) start to become popular and intense debates about how to reflect evolution in classifications created heated discussions.



Ernst Haeckel (1834-1919)



Bessey's “Cactus” (1915)

Placed plant groups with many floral parts in a basal position as the ‘ancestral’ forms.

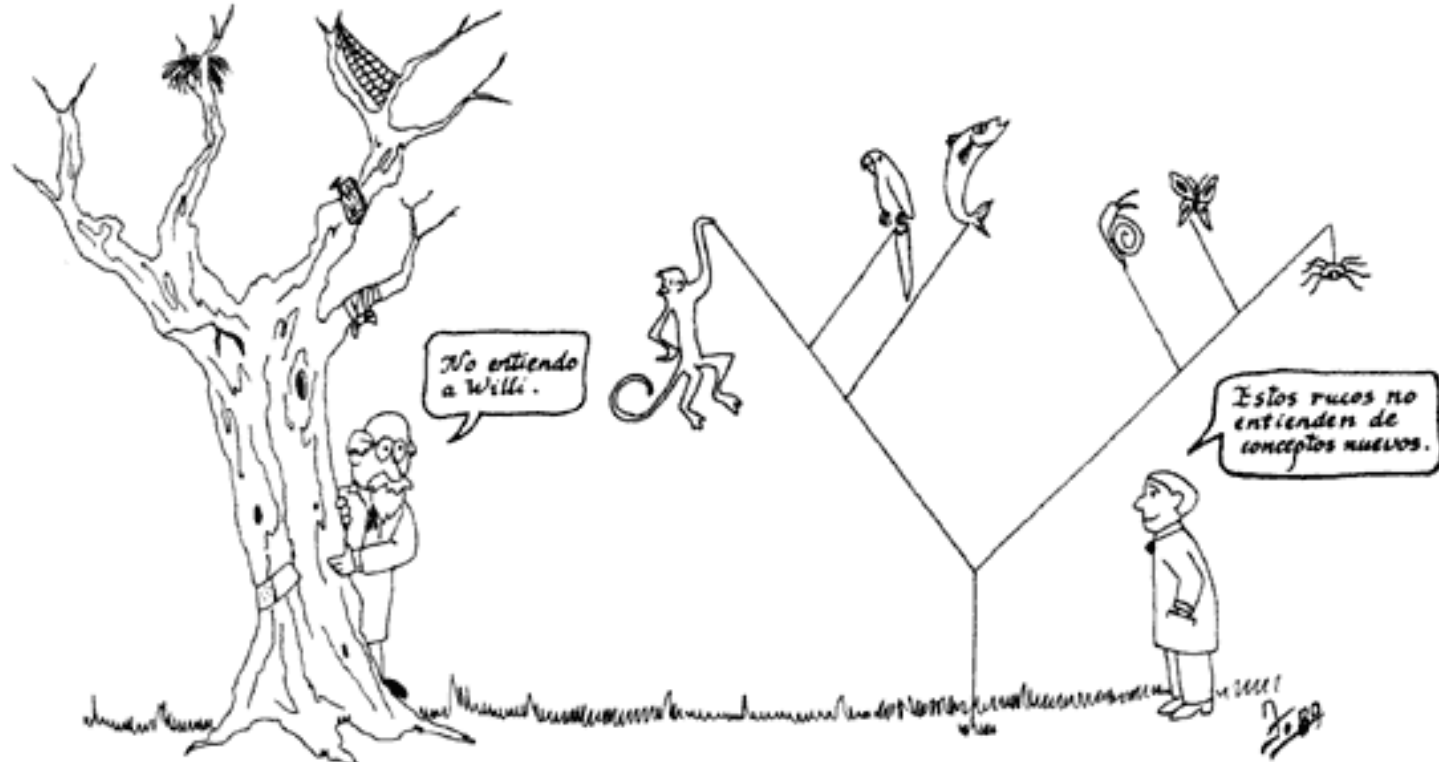
Outlined ‘dicta’ for the construction of phylogenies using the evolutionary trends in character changes.

Polypetalous flowers, insect pollination, cycad-like ancestors

Figure 22-1. Diagram used by Bessey (1915) to illustrate putative relationships among major taxa of the Angiosperms. Used by permission of the Missouri Botanical Garden.

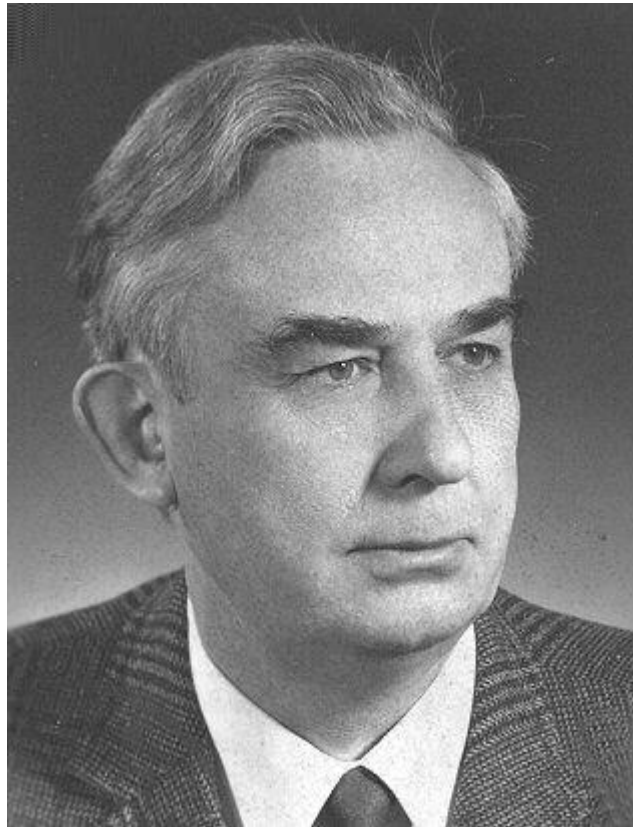
Cladistics (also known as phylogenetic systematics)

Cladistics was born after the publication of Willi Hennig's work (*Grundzüge einer Theorie der phylogenetischen Systematik* 1950), around the time that phenetics became popular.



Cladistics

Hennig's work was not acknowledged until it was translated into English (1966), as a book entitled *Phylogenetic systematics*.



http://commons.wikimedia.org/wiki/File:Willi_Hennig2.jpg

Cladistics: Hennig's basic distinctions

Two types of relationships occur among organisms:

Tokogenetic

With reticulate structure

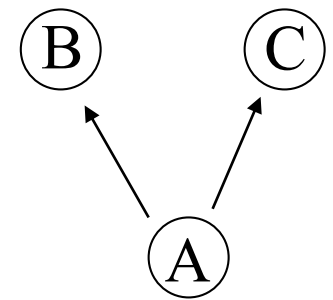
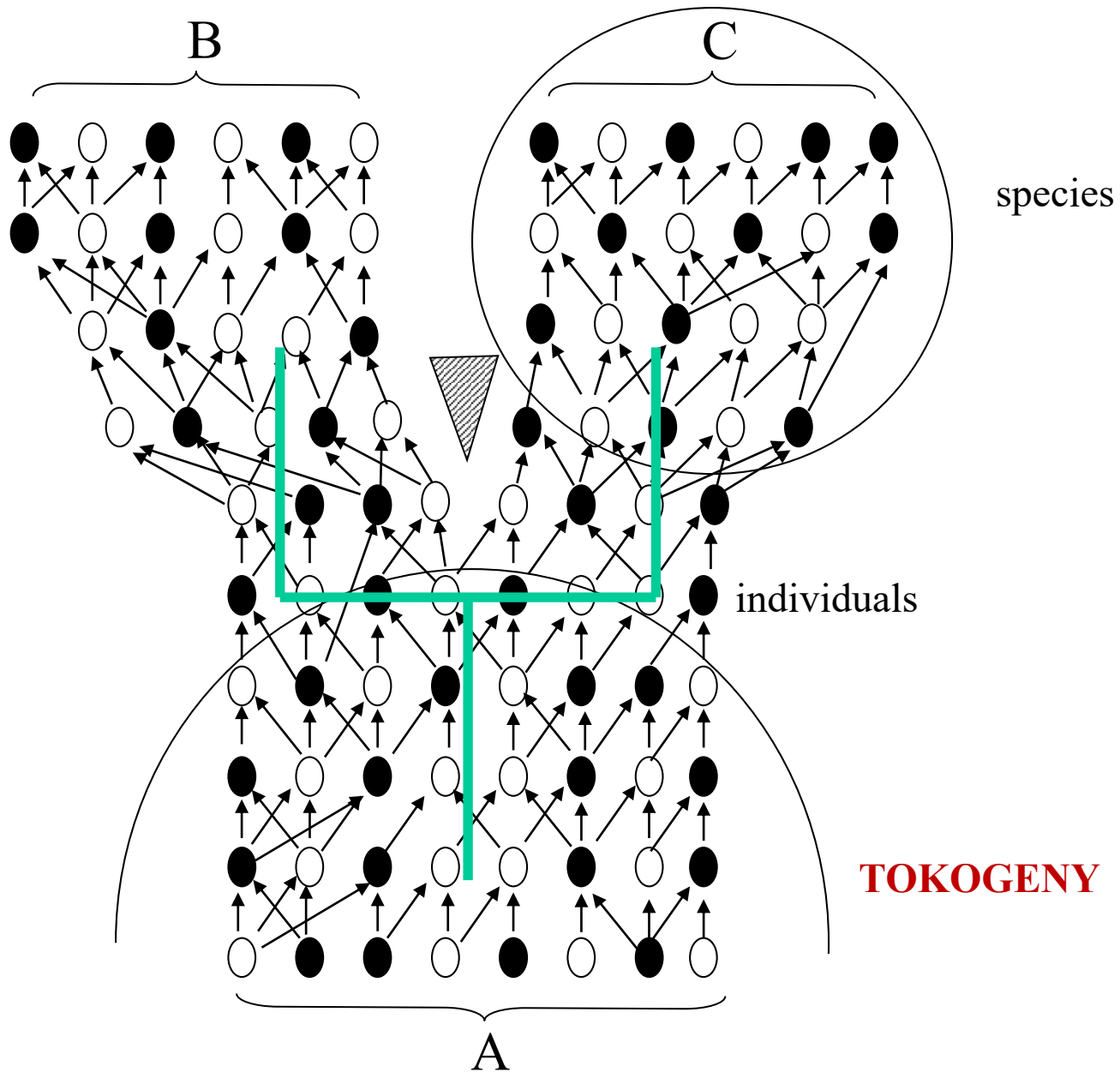
Among individuals (e.g. father-son)

Phylogenetic

At the level of species (ancestor-descendent)

Typically with hierarchical structure

Resulting from descent with modification followed by
genetic isolation



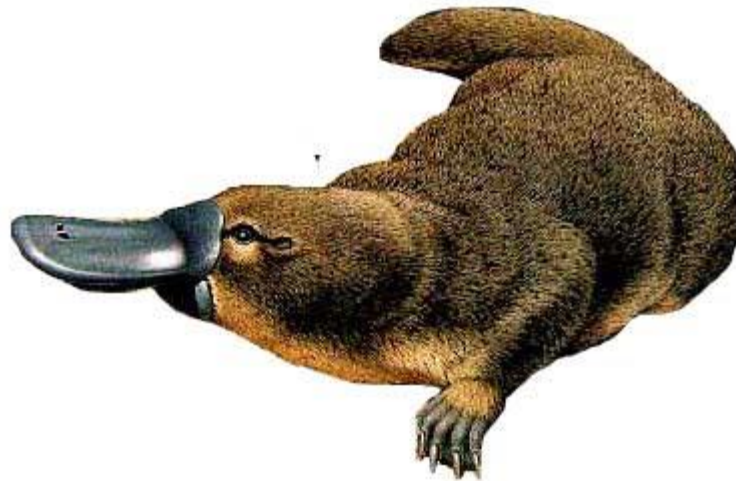
PHYLOGENY

TOKOGENY

Cladistics: Very logical

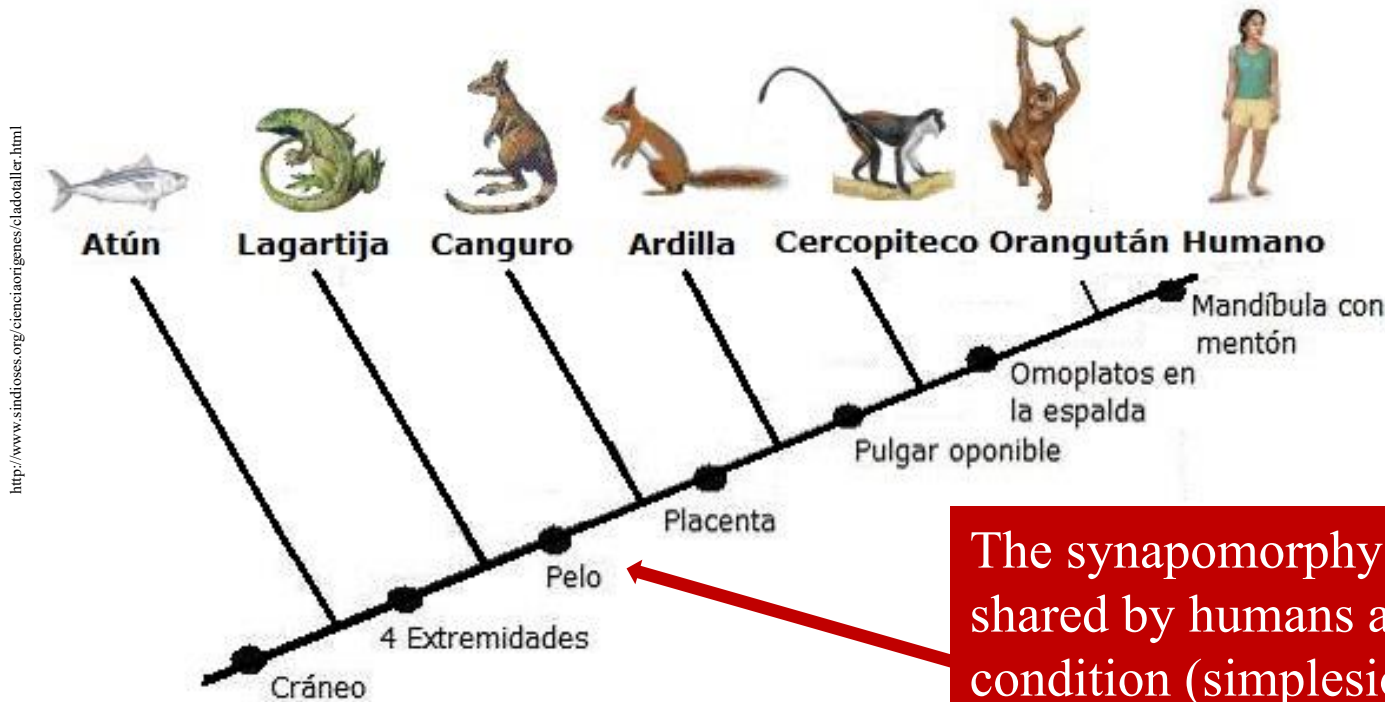
The main driver in evolution is **descendency with modification**

All the species that descend from the same ancestor will have the modification that gave rise to the lineage they belong in; species have shared derived character states (synapomorphies) hierarchically accumulated; they also have the **modifications that gave rise to their particular species (the more recent lineage)**



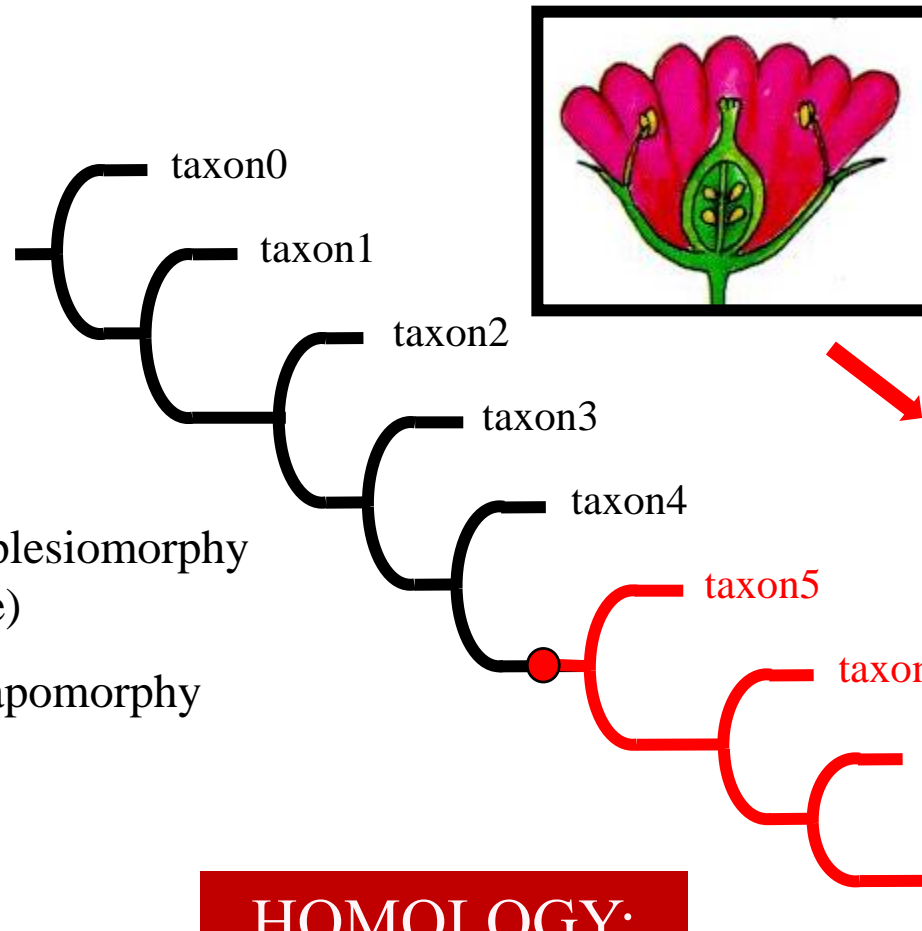
SINAPOMORPHIES (shared derived conditions) provide evidence for different hierarchical relationships

More or less nested synapomorphies help postulating hypotheses about how species are related and how relatively recent the divergency was. Different sets of characters provide evidence at different hierarchical levels depending on when they evolved and how fast the rates of evolution are for that particular character.



The synapomorphy for mammals is shared by humans as an ancestral condition (plesiomorphy)

HOMOLOGY: NOT JUST SINAPOMORPHY

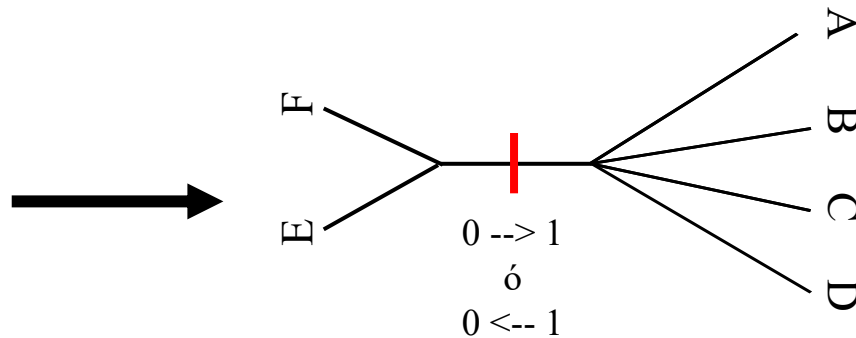


- Similarity due to similesiomorphy (shared ancestral state)
- Similarity due to synapomorphy (shared derived state)

HOMOLOGY:
Similarity due to
common
ancestry

HOMOLOGY vs SINAPOMORPHY

A	1
B	1
C	1
D	1
E	0
F	0

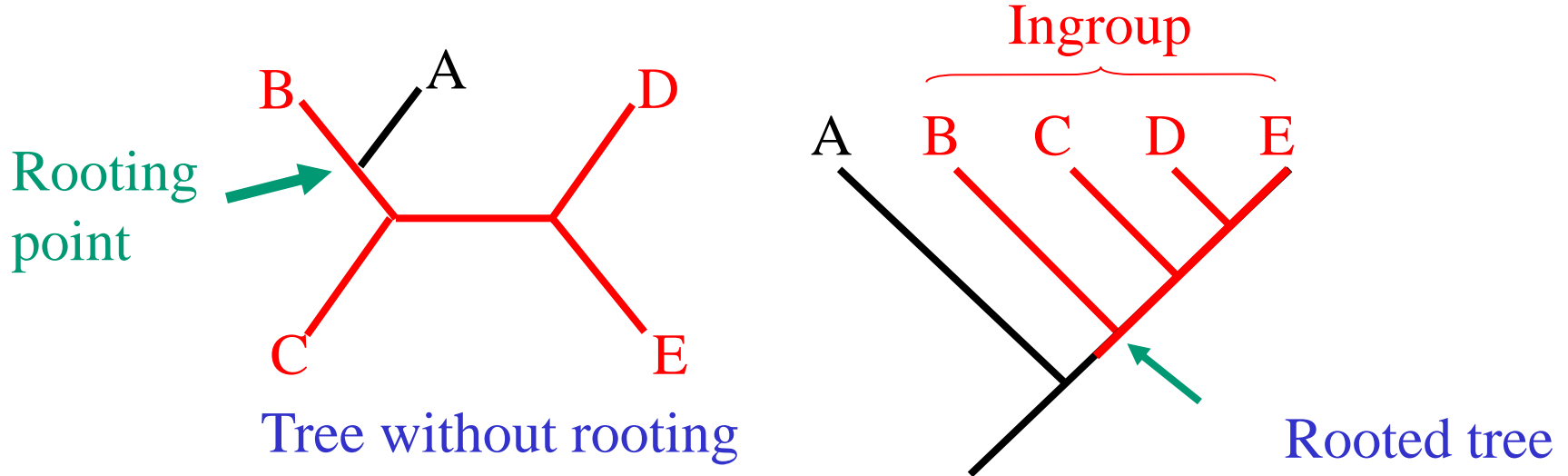


Because both, the ancestral and the derived conditions are hypothesis of homology, it is not necessary to *a priori* know which of the alternative conditions is the derived one and which one is the ancestral: it is the postulation of a change what reflects homoplogy

Groups are not recognized by the synapomorphies but instead by the hypothesis of a single transformation between the alternative observations

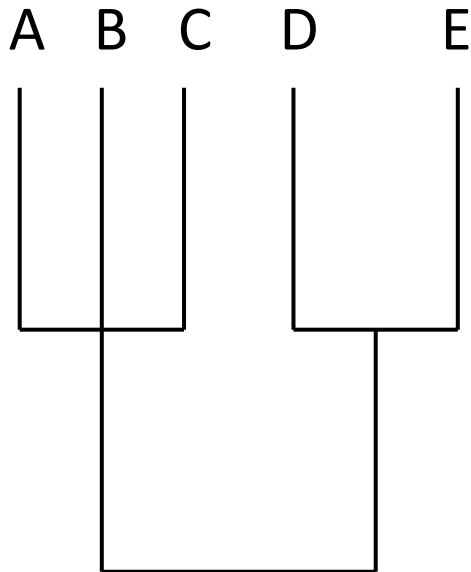
OUTGROUP and character polarity

To interpret the directionality of the character change (the polarity of the character) it is necessary to orient (root) the tree. One could arbitrarily root it between any two internodes, but depending on how the tree is oriented the interpretations of relationships can be very different; therefore, one must include in the analyses taxa that do not belong to the immediate group of interest (outgroup)

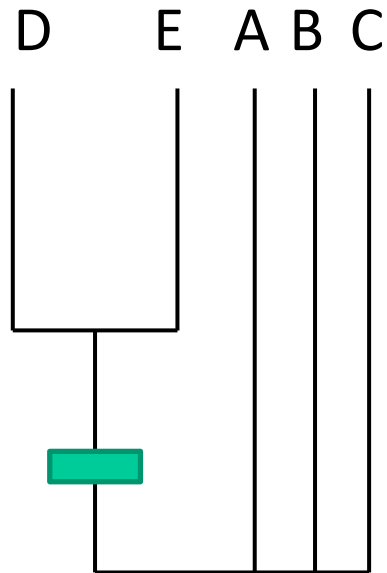


Feneticismo vs Cladismo

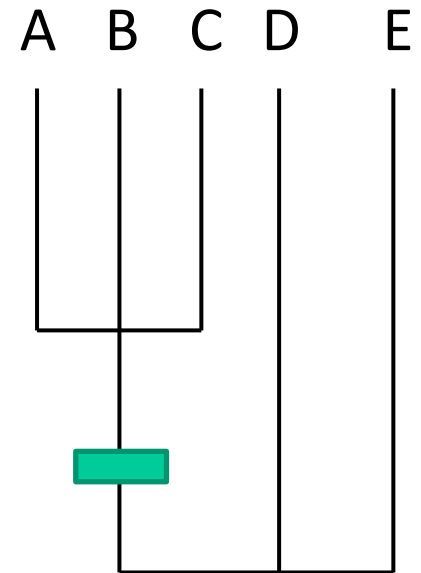
Terminal	Observation
A	0
B	0
C	0
D	1
E	1



Phenetics or
evolutionism



0-->1

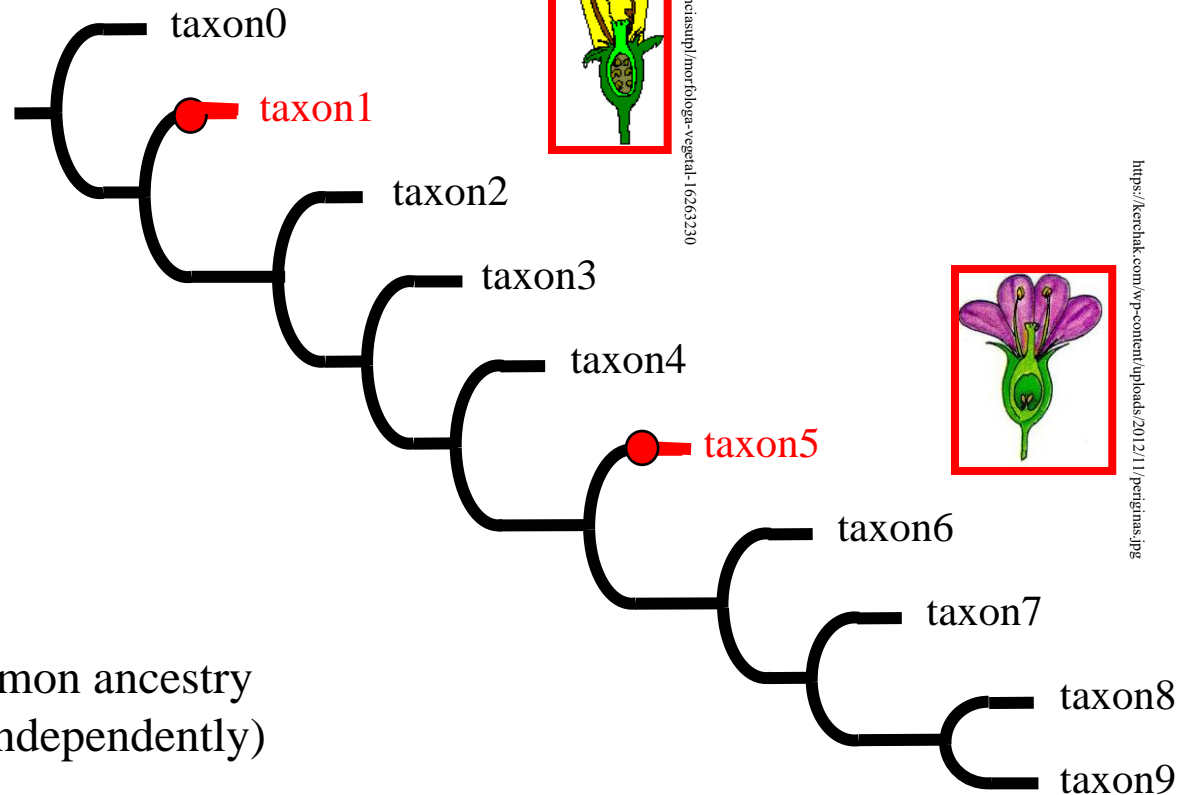


Cladistics

1-->0

Homoplasy

The key is then to distinguish shared derived character states (homology) from independently achieved (derived) character states (homoplasy)



- Similarity **not** due to common ancestry (character states derived independently)

**SIMILITUD CAUSED BY
CONVERGENCY,
PARALLELISM OR
REGRESION**

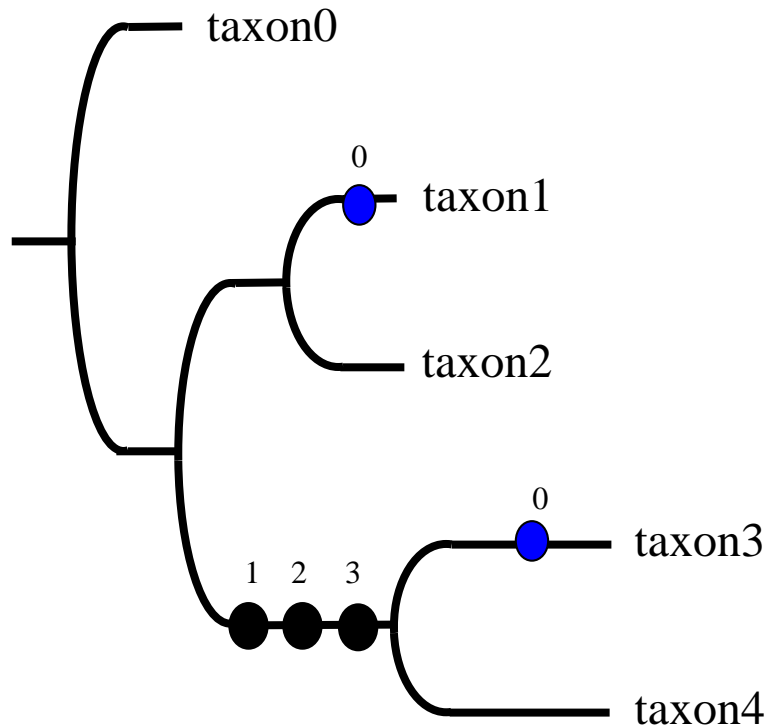
PARSIMONY was proposed for this purposes by Hennig



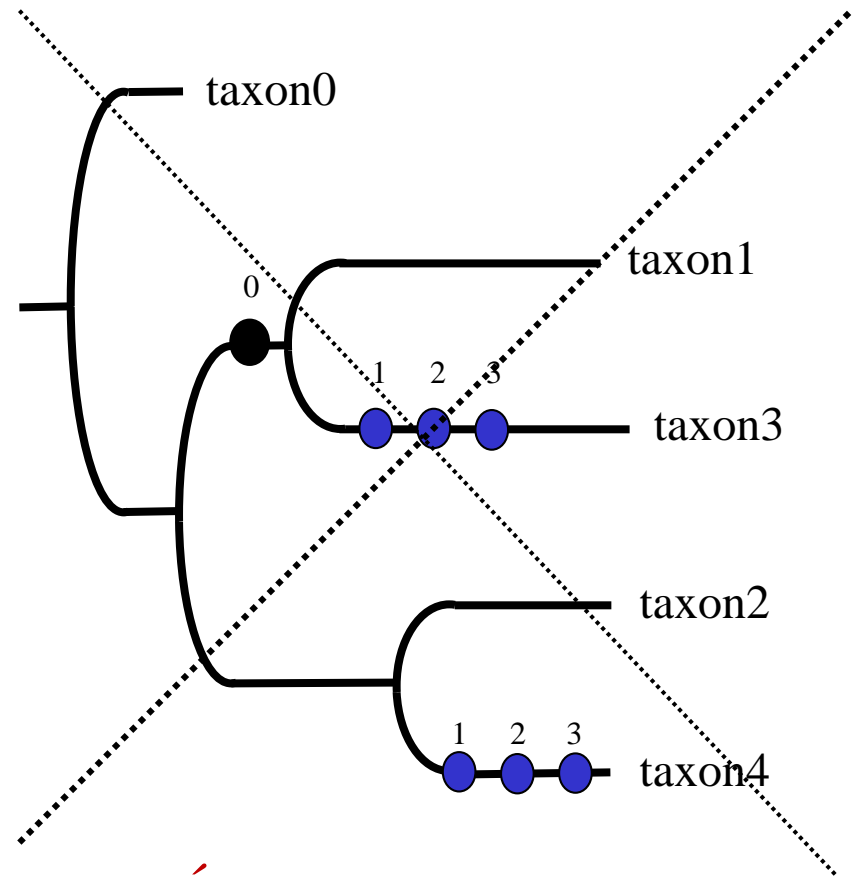
Every comparative observation that can be inherited can be postulated as a homology hypothesis; all hypothesis are subjected to a corroboration/refusal test (parsimony) at once; the tree that implies the least number of changes is accepted as the preferable phylogenetic hypothesis

Parsimony in a scientific context means not to assume more causes than those minimally needed to explain the observations

PARSIMONY: Maximum corroboration of the homology hypotheses (observations)




HIPOTHEESIS 1:
5 changes (more corroboration)



HIPÓTESIS 2:
7 changes (less corroboration)

PROBABILITY BASED ON MODELS

 Likelihood of hypothesis =
 Probability of data given hypothesis

- Fair or unfair coin?

$$P_{\text{head}} = 0.5 \quad \text{Fair}$$

$$P_{\text{head}} = 0.67 \quad \text{Unfair}$$



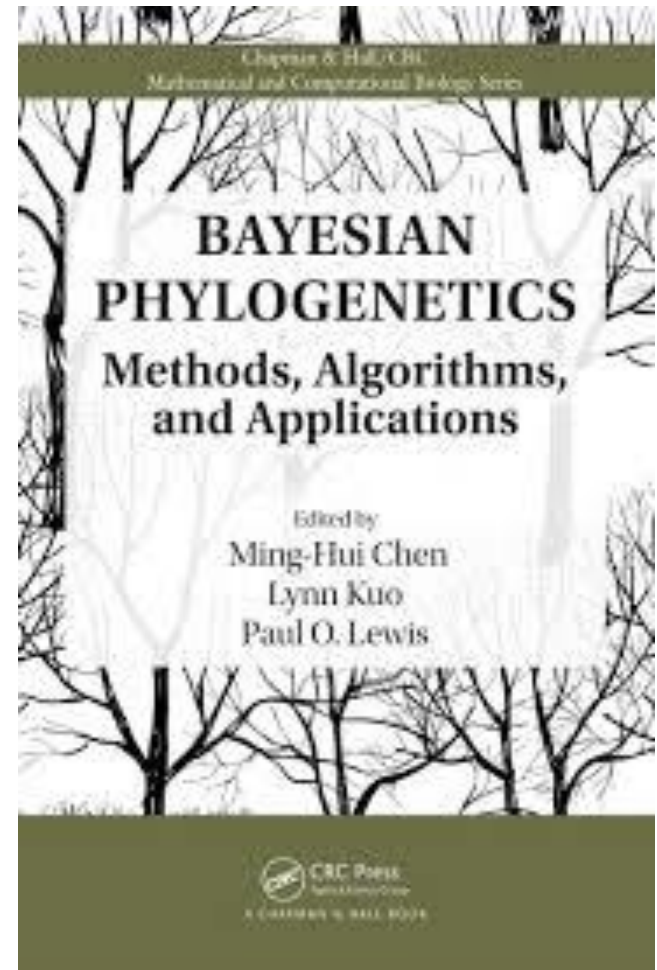
- Flip coin 4 times, get:

3 heads, 1 tail

	Fair	Unfair
H x H x H x T	$1/2 \times 1/2 \times 1/2 \times 1/2 = 1/16$	$2/3 \times 2/3 \times 2/3 \times 1/3 = 8/81$
H x H x T x H	$1/2 \times 1/2 \times 1/2 \times 1/2 = 1/16$	$2/3 \times 2/3 \times 1/3 \times 2/3 = 8/81$
H x T x H x H	$1/2 \times 1/2 \times 1/2 \times 1/2 = 1/16$	$2/3 \times 1/3 \times 2/3 \times 2/3 = 8/81$
T x H x H x H	$1/2 \times 1/2 \times 1/2 \times 1/2 = 1/16$	$1/3 \times 2/3 \times 2/3 \times 2/3 = 8/81$
Total	$1/4$ (0.25)	$32/81$ (0.40)

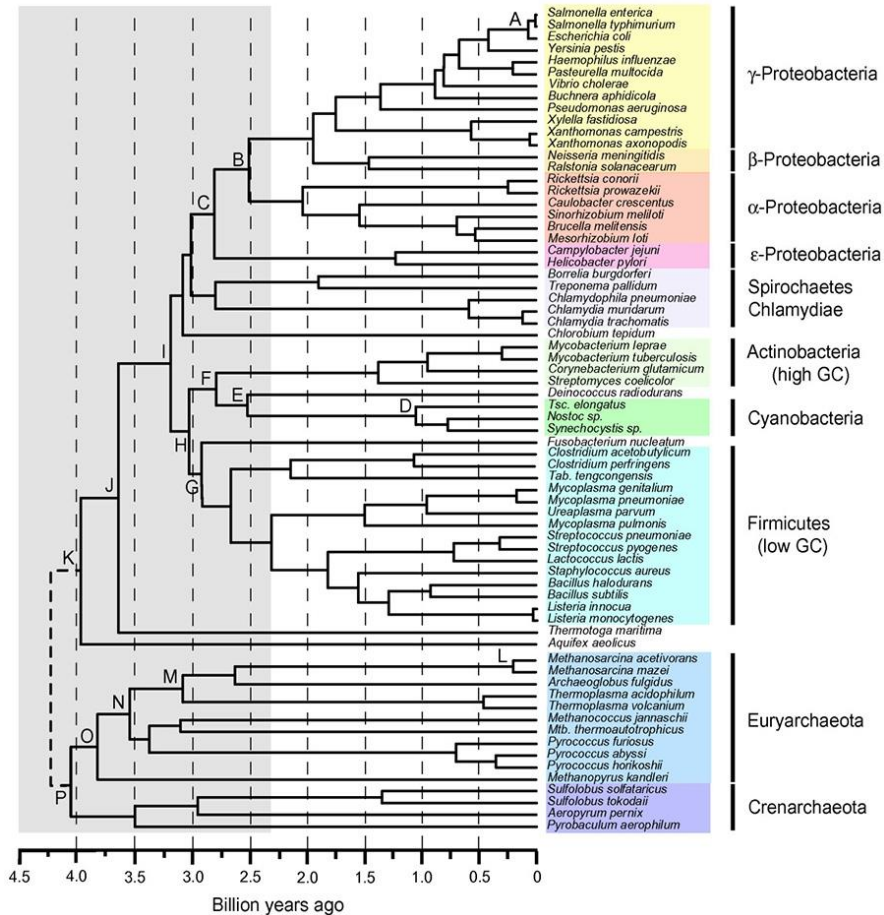
<https://www.ncbi.nlm.nih.gov/Class/NAWBIS/Modules/Phylogenetics/images/phylonv48.gif>

Other methods to choose upon
alternative phylogenetic
hypotheses are now more
frequently used

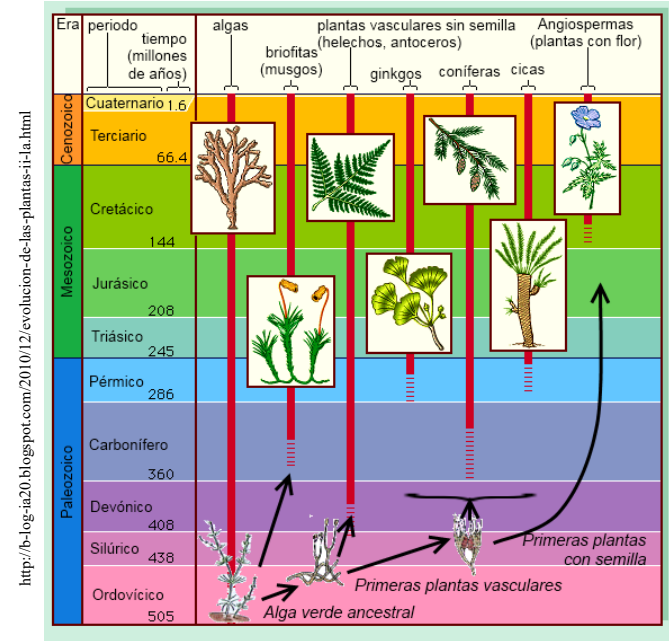


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In phylogenetics the study units are considered as «TERMINALS»



<https://www.visionlearning.com/es/library/Biologia/2/EI-Describe/tema-y-Estructura-de-C%C3%A9lulas/64>



<http://b-log-ia20.blogspot.com/2010/12/evolucion-de-las-plantas-ii-1a.html>

Ancestors are hypothetical
vs.

Terminals are discoverable (like fossils)

TERMINALS in cladistic analyses

Theoretically, any type of terminal can be included in a cladistic analysis

Therefore, the sampling of terminals has to be designed strictly accordingly to the objectives of the study and it will determine, both, the results and their interpretation



TYPE OF TERMINALS

Arbor

Biogeografía cladística: conceptos básicos

Juan J. Morrone

Arbor CLVIII, 623-624 (Noviembre-Diciembre), 373-388 pp.

La biogeografía cladística asume una correspondencia entre relaciones taxonómicas y relaciones de área. Un análisis de biogeografía cladística implica tres etapas: (1) la construcción de cladogramas taxonómicos basados en los cladogramas de los diferentes taxones analizados; (2) la obtención de cladogramas resueltos de áreas, y (3) la obtención de cladogramas generales de áreas basados en la información contenida en los cladogramas resueltos de áreas. Para alcanzar esta última etapa, se disponen de varias técnicas.

Available online at www.sciencedirect.com

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Cladistics 19 (2003) 120-127

www.elsevier.com/locate/jclad

Cladistic analysis of languages: Indo-European classification based on lexicostatistical data

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Accepted 15 July 2003

Abstract

The phylogeny of the Indo-European (IE) language family is reconstructed using a lexicostatistical dataset collected by Dyen (about 200 meanings, 8% outgroup). Three different methods of character coding provide trees (a) the stable position of the Albanian language; (b) the unstable position of the Albanian language; (c) the unstable position of the Balto-Slavonic-Indo-Iranian ("satem") and the Roman compared with the phenetic approach to lexicostatistical data, the results suggest a predominantly branching pattern of individual words. Different scenarios of IE differentiation based on © 2002 The Willi Hennig Society. Published by Elsevier Science (U



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journal homepage: www.elsevier.com/locate/ympev

Review

Integrating phylogenetics, phylogeography and population genetics through genomes and evolutionary theory

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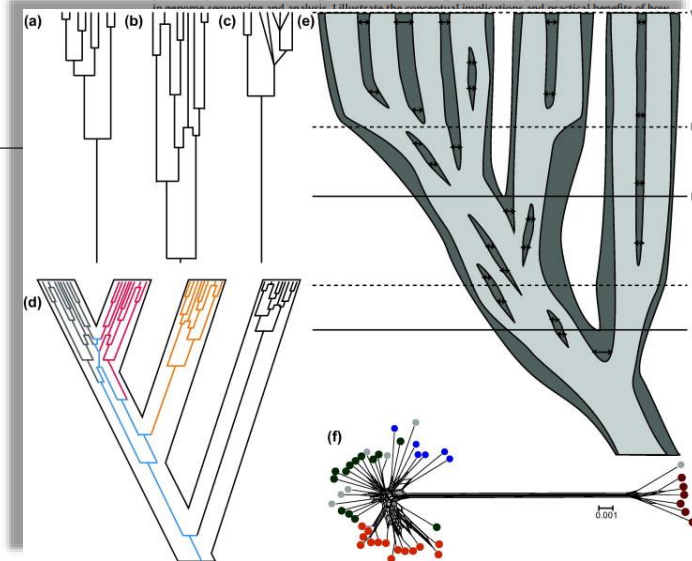
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Speciation
Genome evolution
Coalescent theory

ABSTRACT

Evolutionary theory is primed to synthesize microevolutionary processes with macroevolutionary divergence by taking advantage of multilocus multispecies genomic data in the molecular evolutionary analysis of biodiversity. While coalescent theory bridges across timescales to facilitate this integration, it is important to appreciate the assumptions, caveats, and recent theoretical advances so as to most effectively exploit genomic analysis. Here I outline the connections between population processes and phylogeny, with special attention to how genomic features play into underlying predictions. I discuss empirical and theoretical complications, and solutions, relating to recombination and multifurcating genealogical processes, predictions about how genome structure affects gene tree heterogeneity, and practical choices for genomic data analysis. I illustrate the concepts of gene tree and species tree heterogeneity using



Phylogenetic analyses: potential objectives in the gypworld context

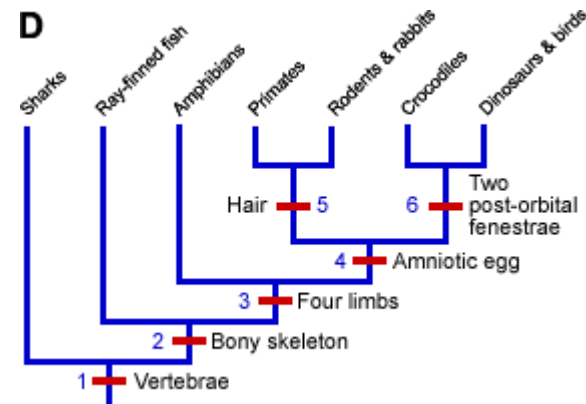
- 1) To know **which is the sister species of a gypsophyte** in order to understand its affinity to/origin in/adaptation to gypsum
- 2) To understand **how & when** the species reached the gypsum habitat(s) in order to understand the origin of the flora
- 3) To identify (morphological) **adaptations** that allow the species to have a better fit to gypsum than outside it
- 4) To explore if different gypsum areas could be connected through **colonisations of already adapted species followed by diversification or de-novo**



If a cladogram is to be interpreted as a phylogeny terminals need to be potential evolutionary units

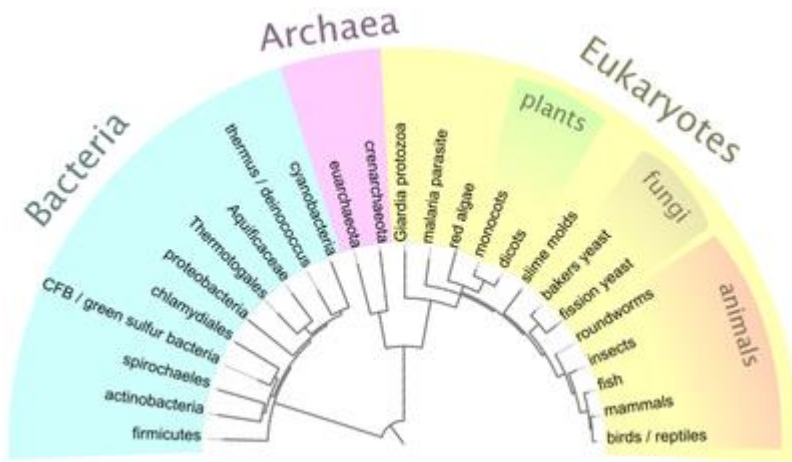
To answer questions like those in the previous slide, one needs to consider terminals as potential evolutionary units and characters as inheritable traits with hypothesized evolutionary transformations: 1) they must be intrinsic; 2) the character states (variations of the trait) must be shared by more than one terminal

	Vertebrae?	Bony skeleton?	Four limbs?	Amniotic egg?	Hair?	Two post-orbital fenestrae?
Sharks and relatives	YES	no	no	no	no	no
Ray-finned fishes	YES	YES	no	no	no	no
Amphibians	YES	YES	YES	no	no	no
Primates	YES	YES	YES	YES	YES	no
Rodents and rabbits	YES	YES	YES	YES	YES	no
Crocodiles and relatives	YES	YES	YES	YES	no	YES
Dinosaurs and birds	YES	YES	YES	YES	no	YES

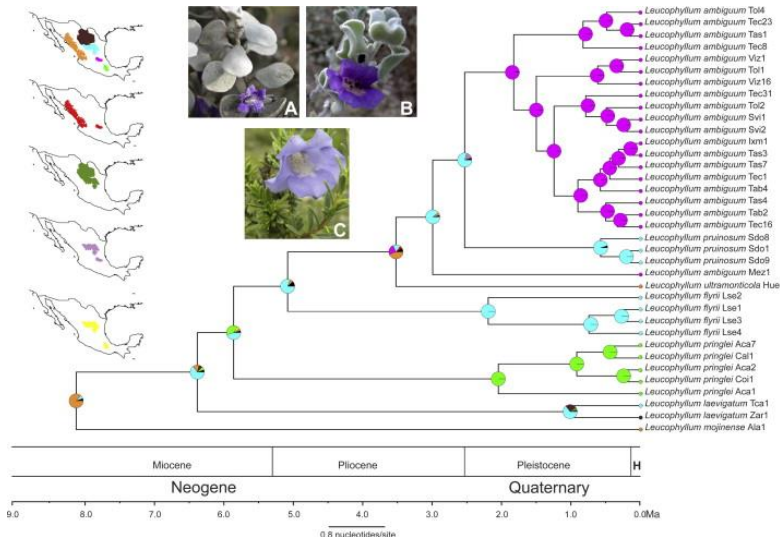
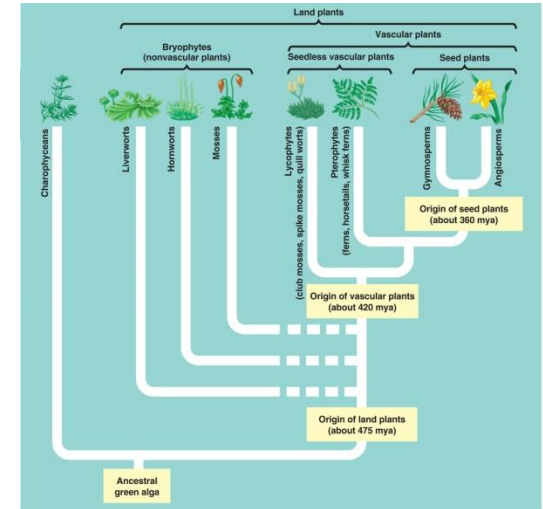


TERMINALS can cover different hierarchical levels

Phylogenetic analysis can use individuals, populations, species, genera, families, etc. as sampling units



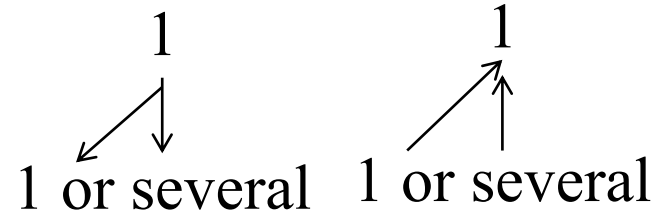
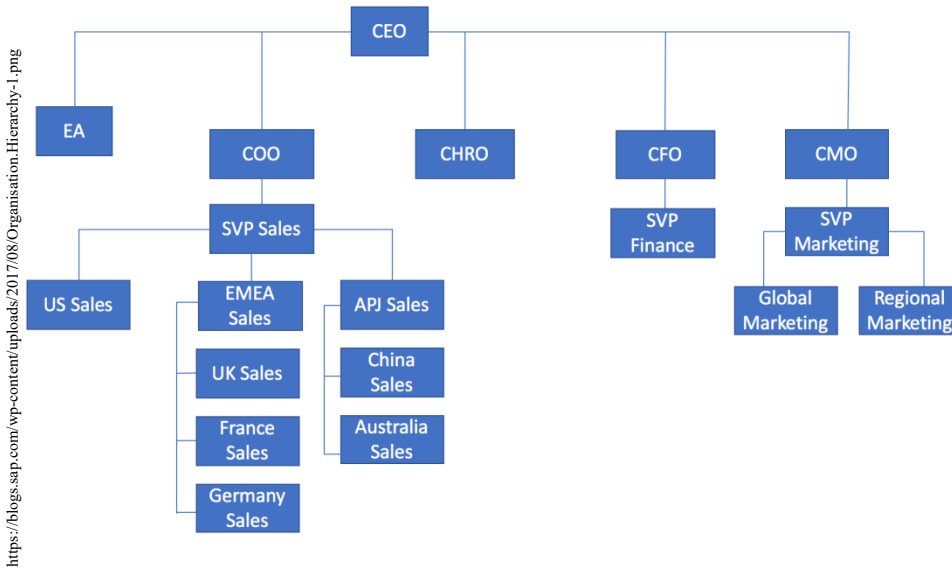
https://upload.wikimedia.org/wikipedia/commons/thumb/e/e6/Simplified_tree.png/400px-Simplified_tree.png



<https://ars.els-cdn.com/content/image/1-s2.0-S1055790314000931-gr3.jpg>

TOKOGENY & PHYLOGENY

In general, tokogenetic relationships **do not** produce **natural** hierarchical structure, while phylogenetic relationships normally result in **natural** hierarchical structure



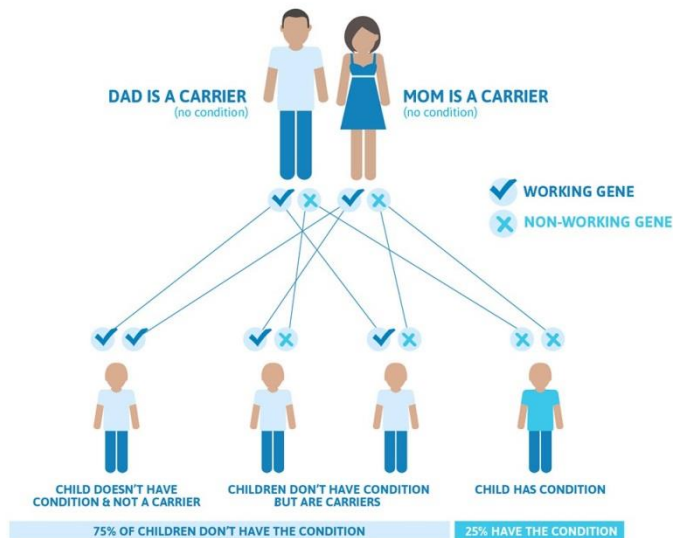
Hierarchy: a structure that is established with a subordination criterium

TYPE OF TERMINALS

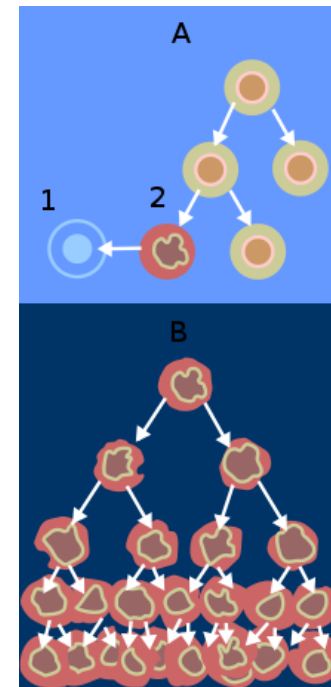
According to Hennig's model, the **appropriate terminals for phylogenetic studies are those that replicate** (and hence produce hierarchical patterns)

Replication implies clonal reproduction or total inheritance

Autosomal Recessive Inheritance Pattern

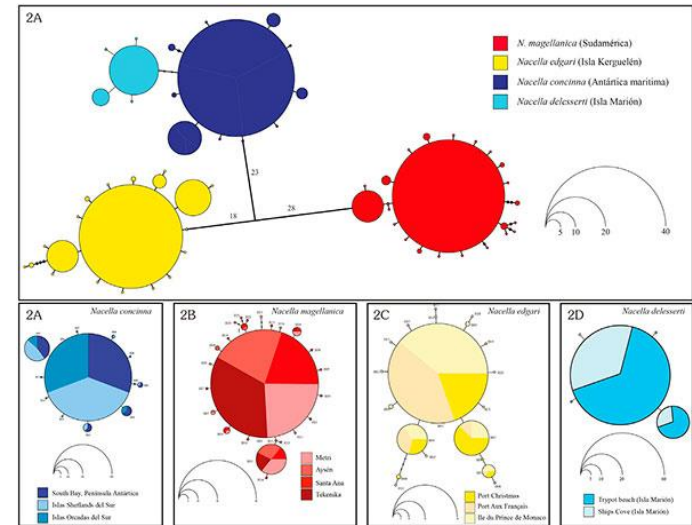


VS



TOKOGENY vs PHYLOGENY

Because **TOKOGENETIC** relationships are normally reticulated, the study of relationships among individuals of the same species is normally conducted through phylogeographic methods, rather than phylogenetic methods

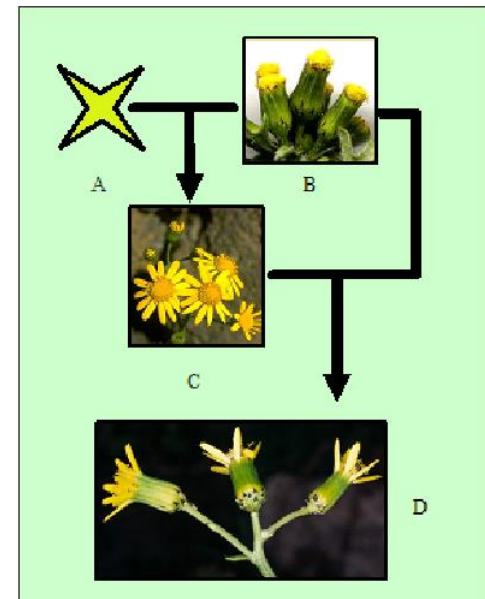
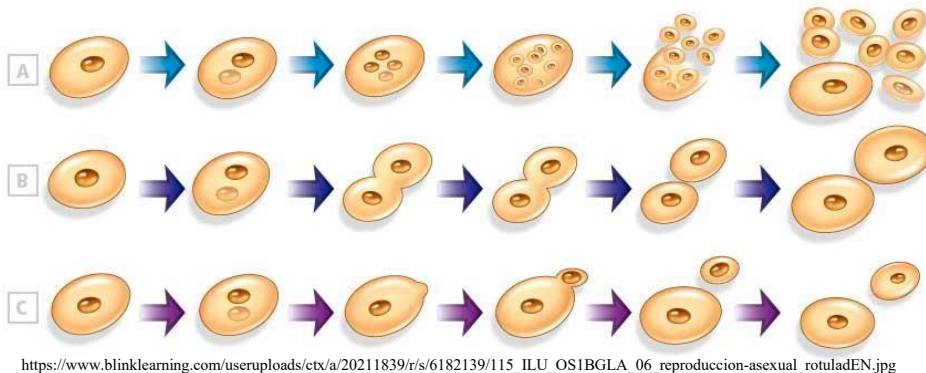


https://scielo.conicyt.cl/scielo.php?script=sci_arttext&pid=S0718-686X2016000300005

Haplotypes of markers with fast evolving rates (such as microsatellites) using methods allowing networks reconstructions are the most commonly used in these cases

TOKOGENY & PHYLOGENY

Despite the common rule of thumb, tokogenetic relationships may produce hierarchical structure (e.g., those among bacteria) and phylogenetic relationships may **not** necessarily result in hierarchical structure (e.g., if there is hybridization)



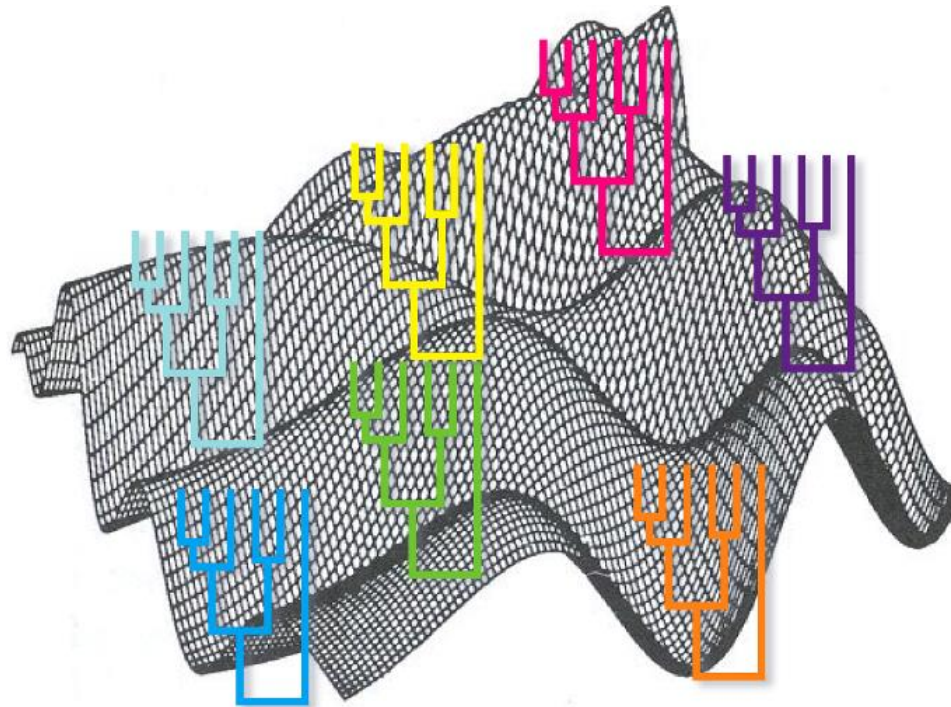
<http://www.iich.com/evolucion/evolucion/la-antitesis-neodarwinista-y-otros-ensayos-breves-sobre-evolucion>

i.e., both, tokogeny and phylogeny, in both cases, the process and the pattern, may or may not be hierarchical

Phylogenetic methods: **TYPE OF TERMINALS**

Phylogenetic methods group morphoclines assuming a hierarchical pattern:

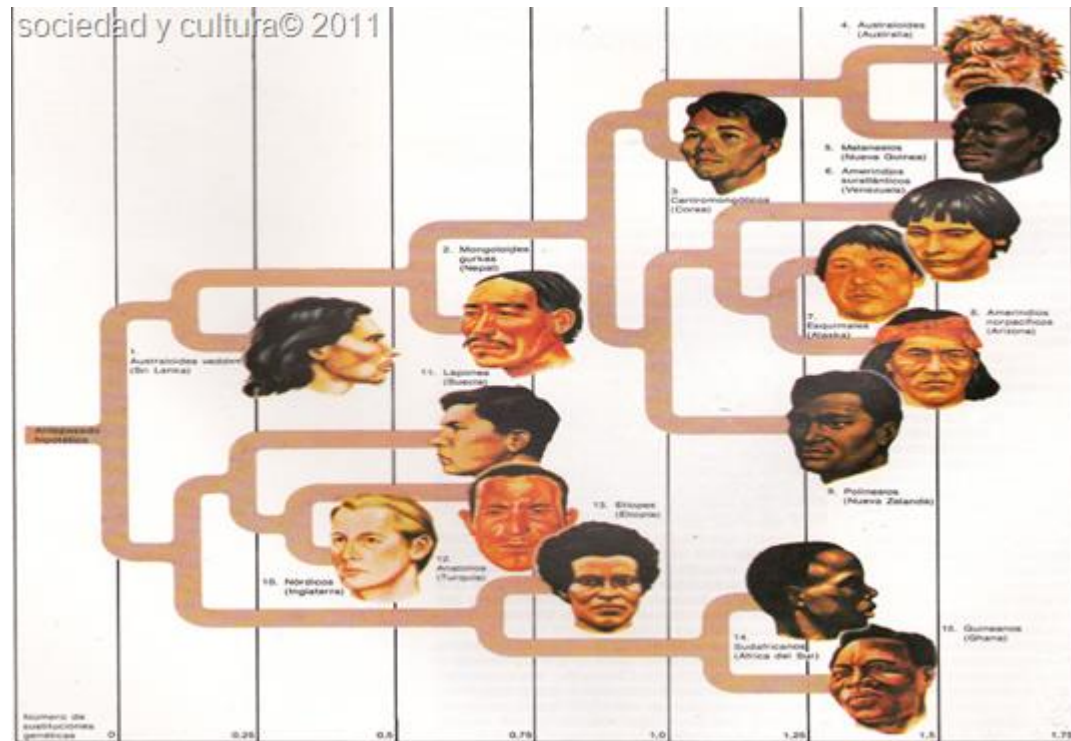
Parsimony explicitly groups morphoclines in such a way that the number of origins is minimized, but probabilistic methods (Likelihood or Bayesian), generally also result in resolution (hierarchical patterns), independently on the type of relationships that the terminals had (tokogenetic or phylogenetic)



TYPE OF TERMINALS

Consequently, analyses that use units below species (intraspecific terminals, such as individuals) can also result in hierarchical patterns, even when the relationships among the terminals (the process) should not naturally produce hierarchies

How to interpret these patterns?



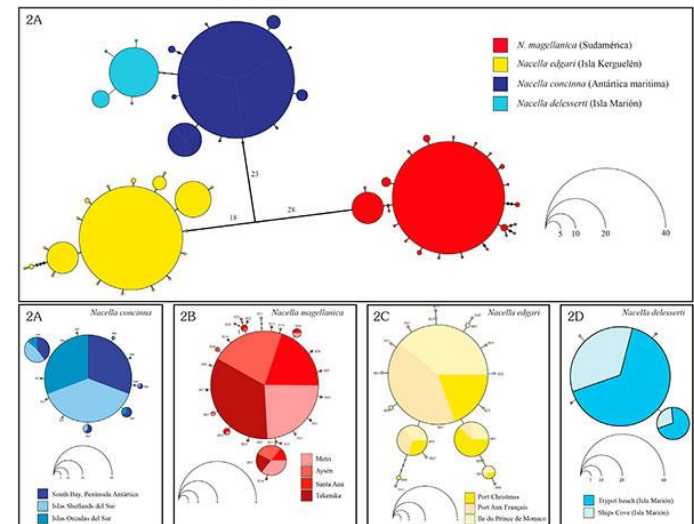
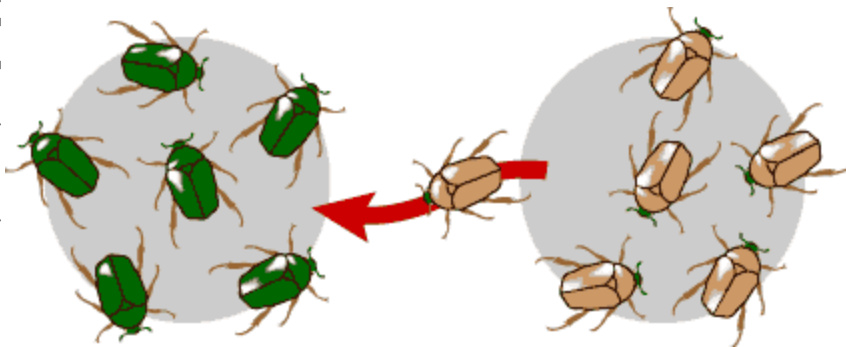
TYPE OF TERMINALS

A hierarchical pattern results from the elimination of possible combinations among terminals during the evolution **or the sampling**

It can be caused by **genetic drift**, **lack of recombination**, **small population sizes** or **INCOMPLET SAMPLING**

Hence, the branches in a **cladogram** can be interpreted as **total divergeny (phylogeny)**, **genic flou**, or **partial divergeny**

https://evolution.berkeley.edu/evolibrary/article/_0evo_21_sp

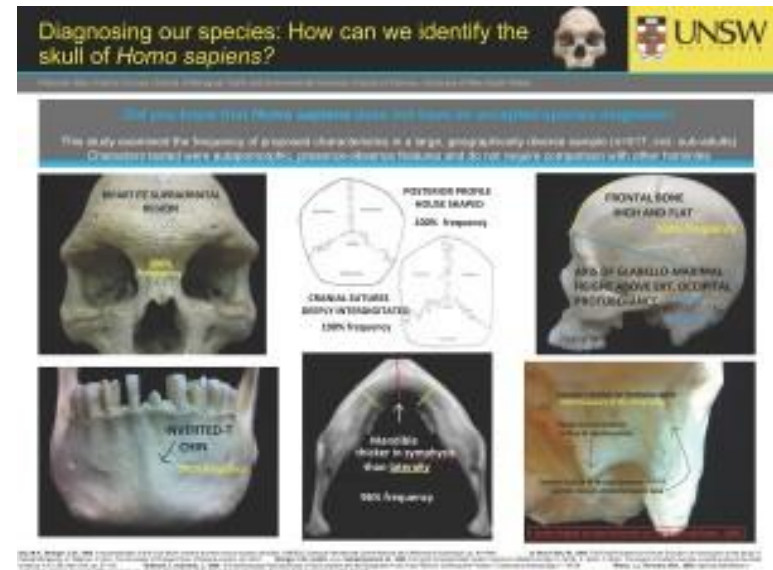


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SAMPLING DENSITY: How many units to include?

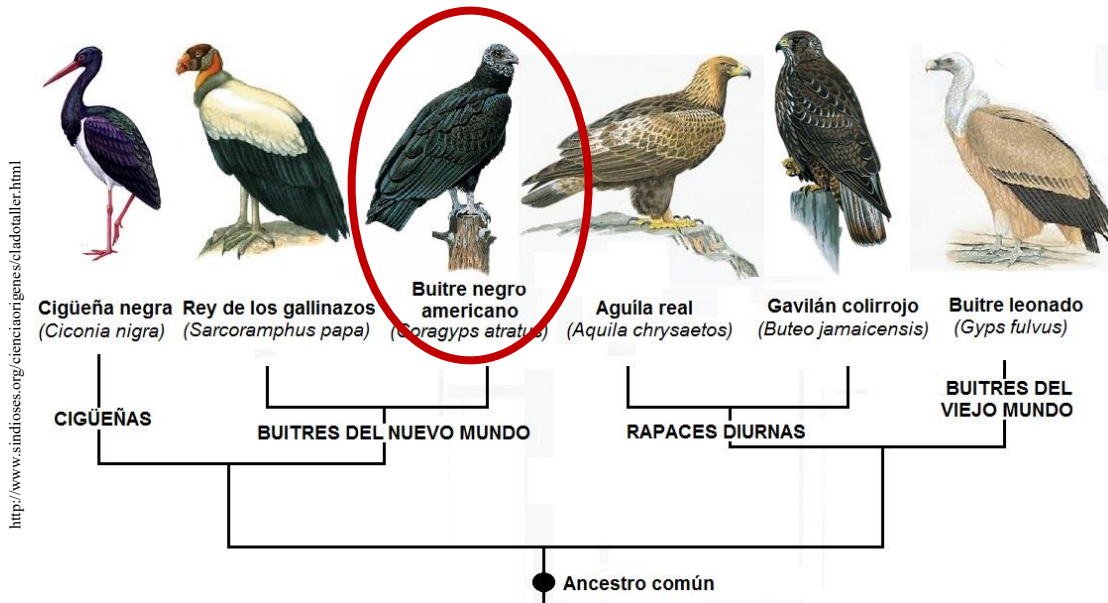
In general, **sampling density affects more drastically the results when individuals are used as terminals than when species or supraspecific taxa are used** (even when they are represented by individuals)

This is because species and supra-specific taxa are mainly or exclusively circumscribed using fixed characters, which therefore are present among the terminals independently of their sampling density



TYPE OF TERMINALS

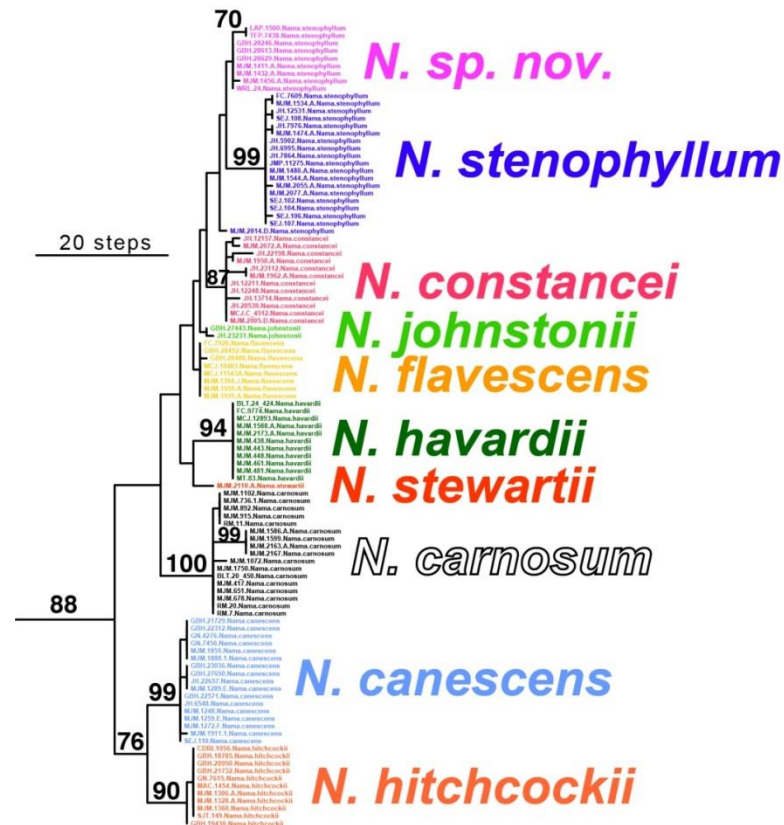
If a cladogram/tree is to be interpreted as a phylogeny, the terminal units that are included **or represented** **MUST** be **species or supra-specific taxa**, which normally have phylogenetic relationships resulting in **total diverging evolutionary units** producing hierarchical patterns



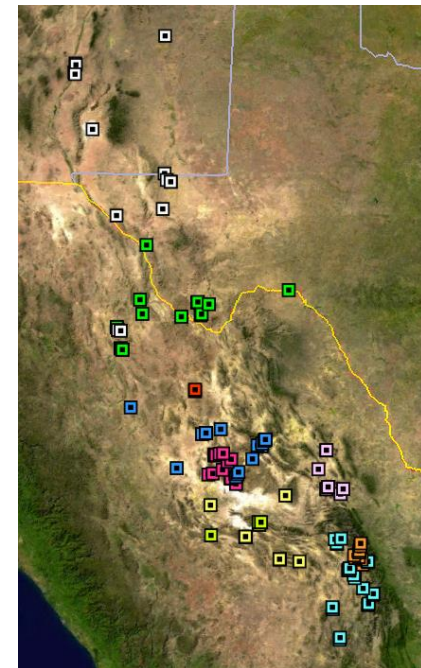
SAMPLING DENSITY: How many units to include?

If the sampling of individuals **and characters** is dense enough, the problem of using a phylogenetic method for non-fixed haplotypes can be overcome as synapomorphies should prevail to group individuals of the same species due to common ancestry

In this case, **trees** can be interpreted as phylogenies using individuals as terminal units

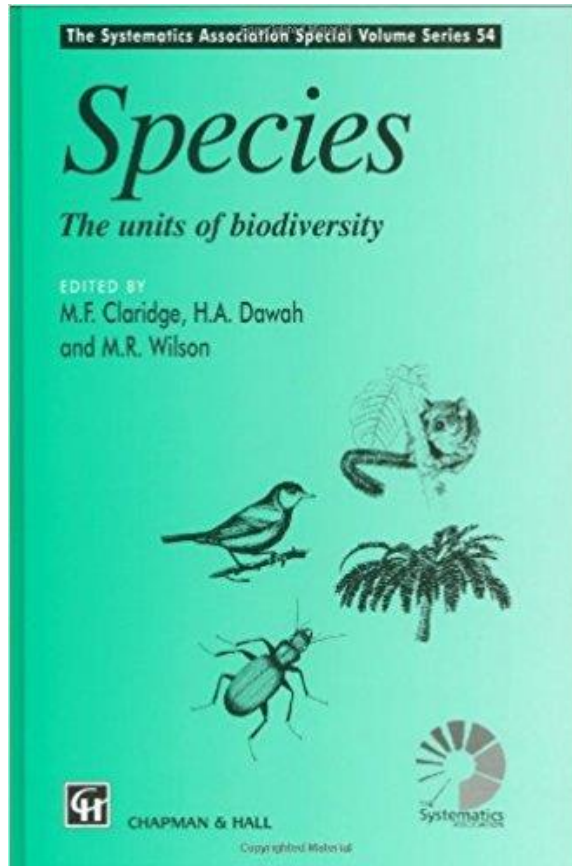


GENETIC DIVERSITY IN NAMA



SPECIES CONCEPT

To interpret a cladogram/tree as a phylogeny one must take into consideration (or imply) a species concept that is compatible with Hennig's principles



Morphologic species

Nominalistic species

Biological species (Dobzhansky, 1935; Mayr, 1942)

Ecological species (Van Valen, 1976): a species is a set of organisms adapted to a particular set of resources, called a niche, in the environment. According to this concept, populations form the discrete phenetic clusters that we recognize as species because the ecological and evolutionary processes controlling how resources are divided up tend to produce those clusters.

http://www.blackwellpublishing.com/ridley/a-z/Ecological_species_concept.asp

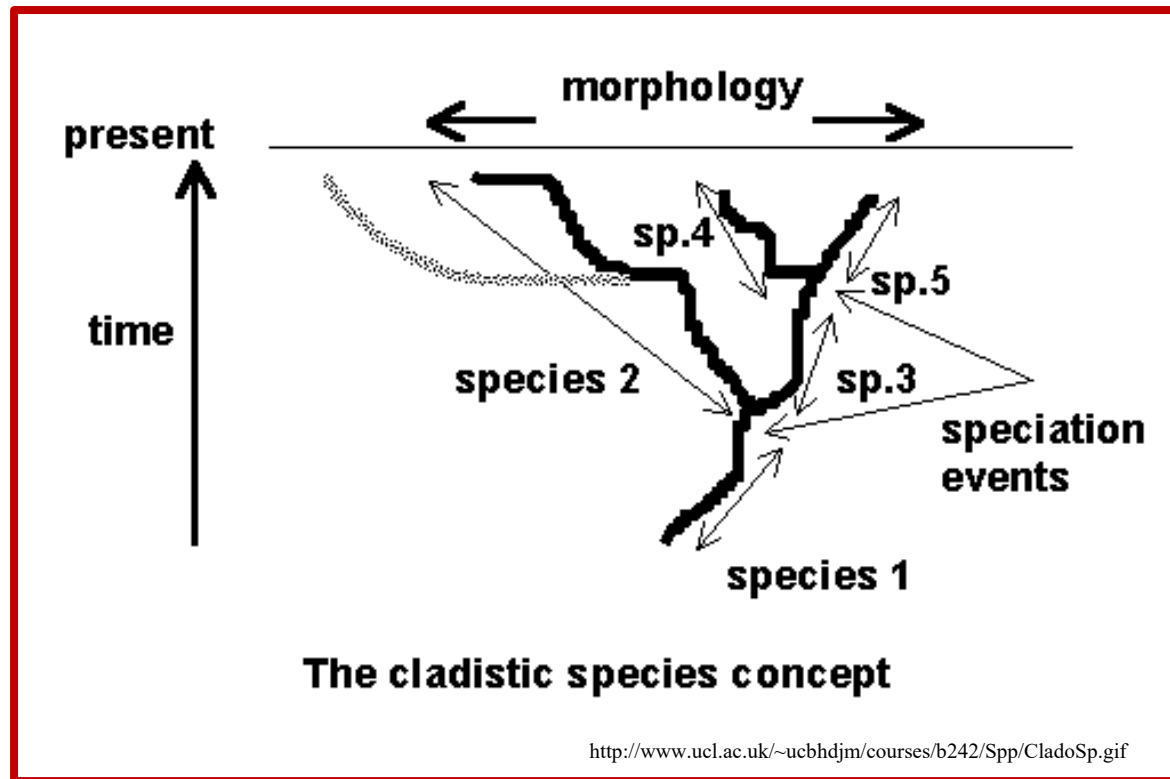
Evolutiary species (Wiley, 1978)

Phylogenetic specie (Cracraft, 1989)

SPECIES CONCEPT

GOOD NEWS: they (almost)all are

Therefore the species concept normally has no major effect in the implementation of the phylogenetic method



TYPE OF TERMINALS

However, it must be understood that the study units (terminals) need to be defined before doing a phylogenetic analysis according to the objectives, because they will determine the interpretation of the results



TWO SETS OF TERMINALS

After deciding which hierarchical level is appropriate for the question we want to answer (individuals, populations, species, etc.), the second important research design has to do with the what we call the ingroup and the outgroup

GYPSOPHYLES
GYPSOCLINES
GYPSOVAGES
GLICOPHYTES

ASPERULA
GALLIUM
PSYCHOTRIA
PLUMERIA



OUTGROUP: definition

An outgroup is the taxon or taxa that does not belong to the group of immediate interest

e.g., the outgroup in an analysis of species from the genus *Pinus* could be *Taxodium*, a *Magnolia* species, a fern, an animal or simultaneously all of the above

<http://miscosaddebrujaiblog.blogspot.mx/2016/05/mis-arboles-de-bruja-el-pino.html>



<http://www.arbolesornamentales.es/Taxodiummucronatum.htm>



<https://www.gardeningknowhow.com/ornamental/trees/magnolia/southern-magnolia-trees.htm>

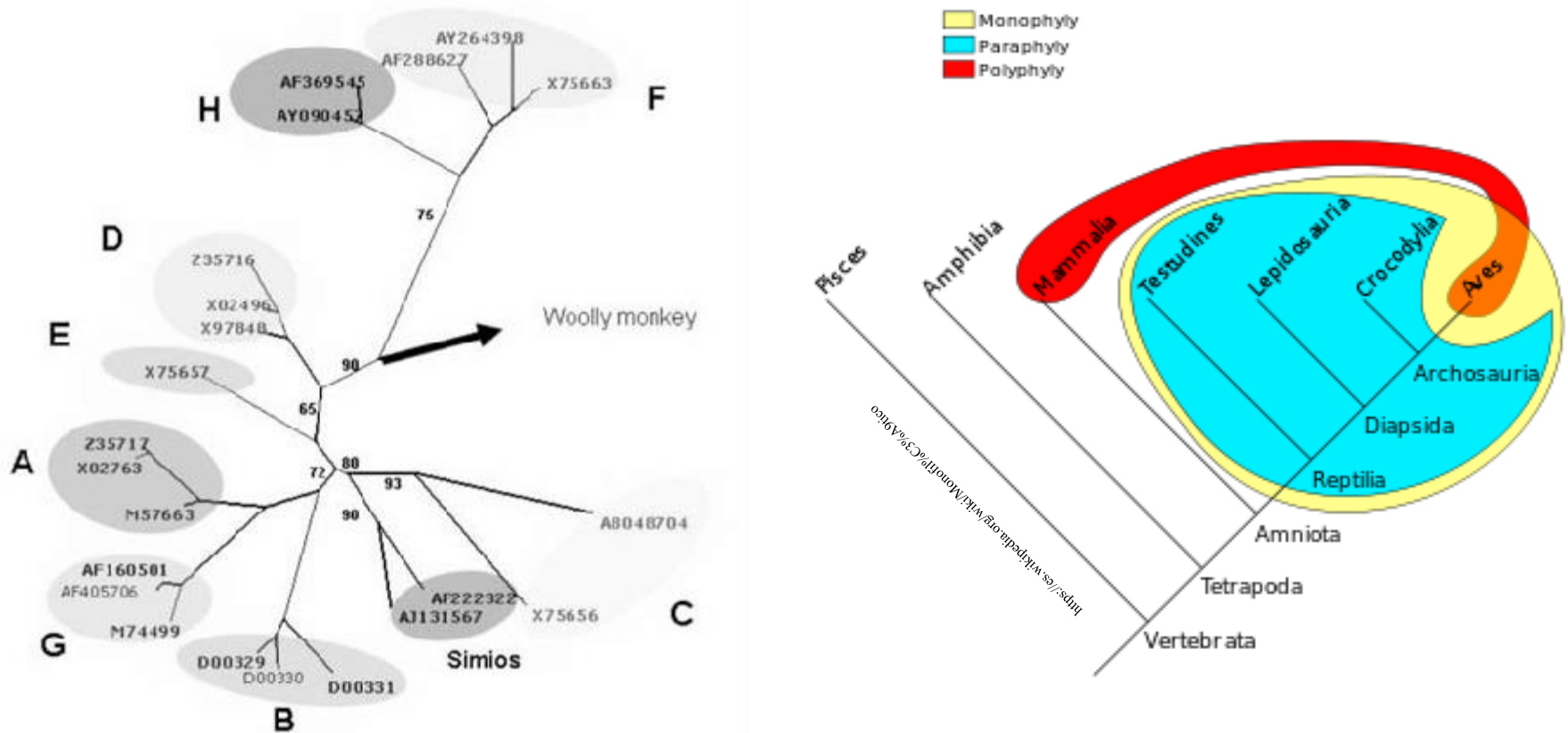


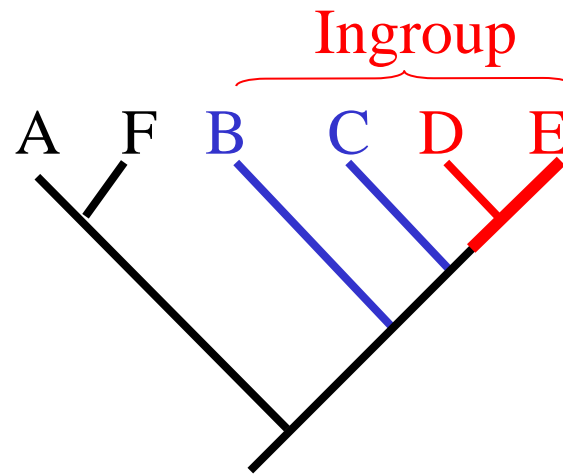
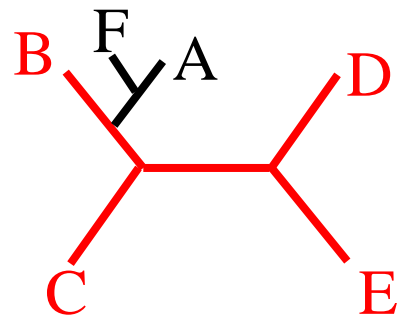
http://proexpansion.com/es/articulos_oe/406-el-laberinto-del-armadillo-gigante

OUTGROUP: objective

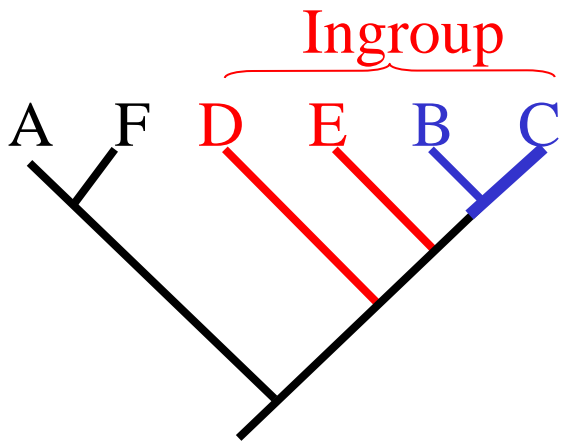
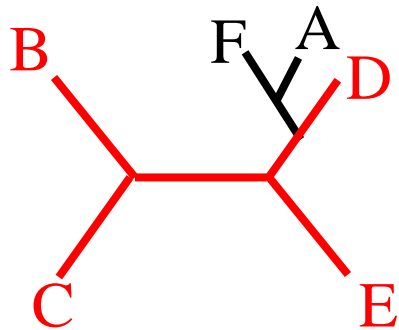
The outgroup in phylogenetic analysis fulfils two main objectives:

- To orient (root) the tree
- To test the monophyly of the group of interest





(BC) paraphylletic
(DE) monophylletic



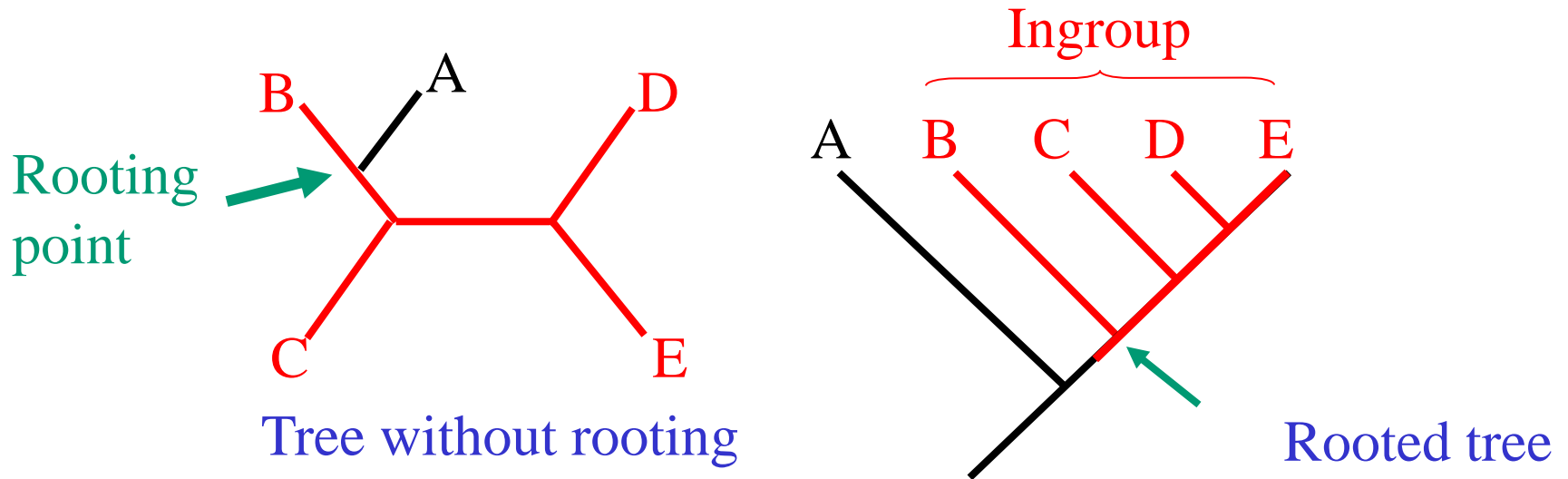
(DE) paraphylletic
(BC) monophylletic



OUTGROUP: function

If the analysis includes **only a single terminal as outgroup**, the tree will be arbitrarily oriented (rooted) between it and the ingroup

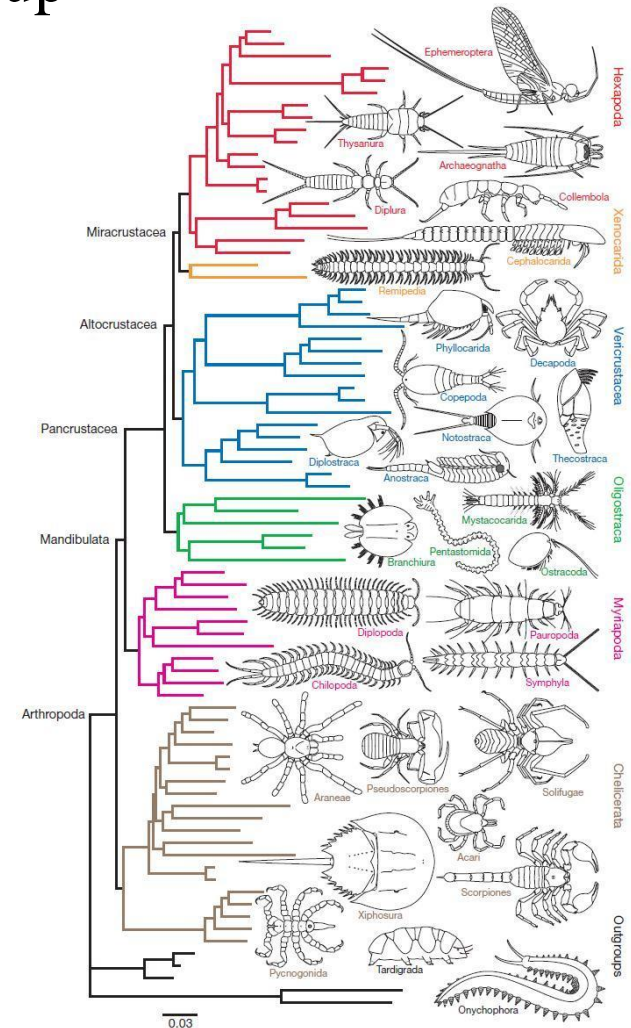
Consequently, the monophyly of the ingroup will not be tested



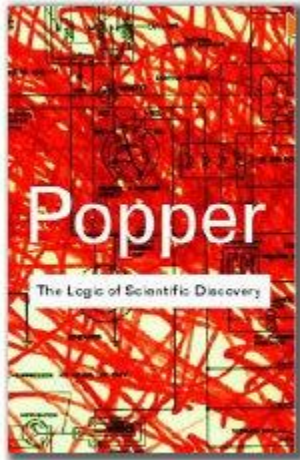
OUTGROUPS & monophyly

The monophyly hypothesis of the ingroup **CAN ONLY** be tested if more than one terminal (taxon) is simultaneously included in the analysis as outgroup

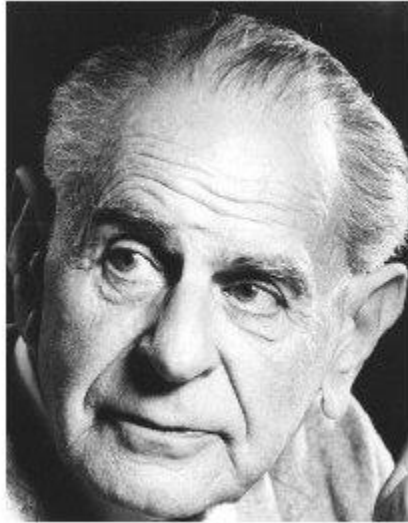
To do this, it is necessary to **include ALL** the members of the outgroup in the matrix together with those of the ingroup (as if there was no difference among them); characters must be gathered and codified for all terminals included in the matrix



OUTGROUP: the best selection seeks for rigor



<http://sqapo.com/popper.jpg>



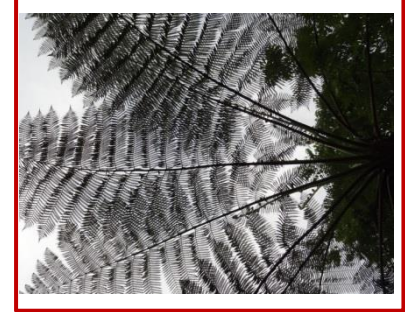
According to Popper's philosophy, our confidence in the results will increase if we try to reject the hypothesis and still it is accepted



<http://miscosadasdebrujablog.blogspot.mx/2016/05/mis-arboles-de-bruja-el-pino.html>

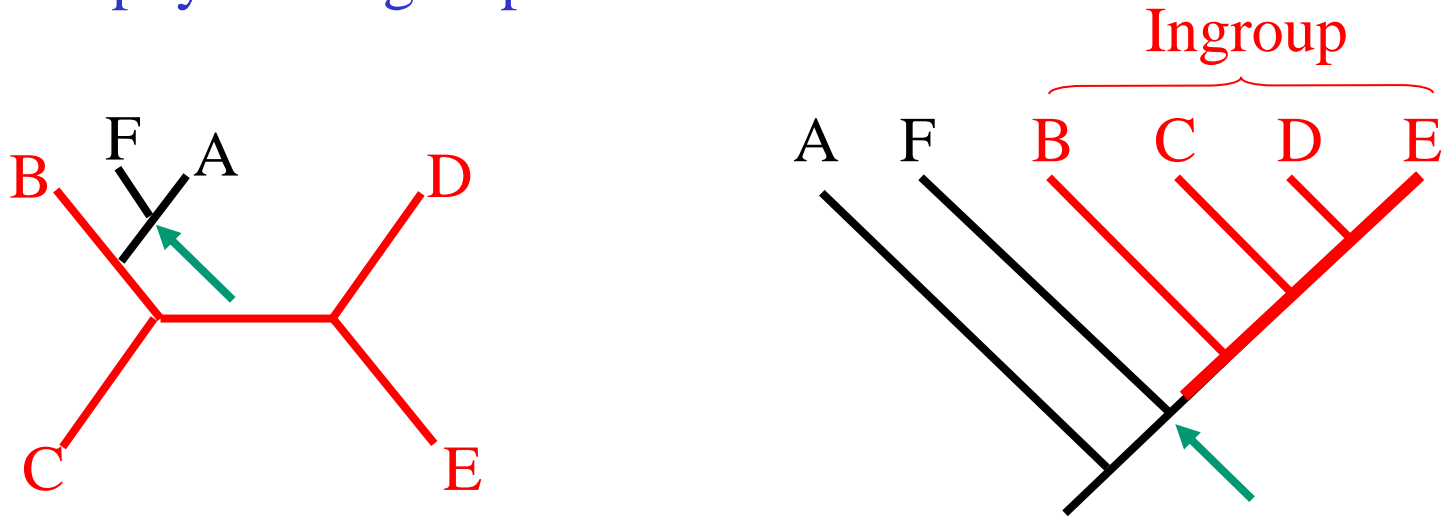


<http://www.arbolesornamentales.es/Taxodiummucronatum.htm>



<https://www.gardeningknowhow.com/ornamental/trees/magnolia/southern-magnolia-trees.htm> http://proexpansion.com/es/articulos_oe/406-el-laberinto-del-armadillo-gigante

Monophyletic ingroup



T. Gamble et al. • New trans-Atlantic gecko clade

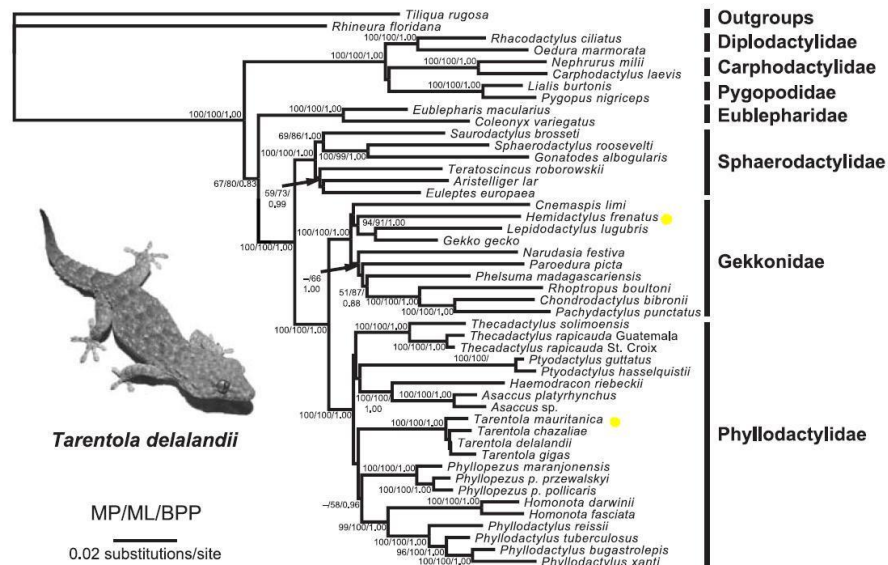
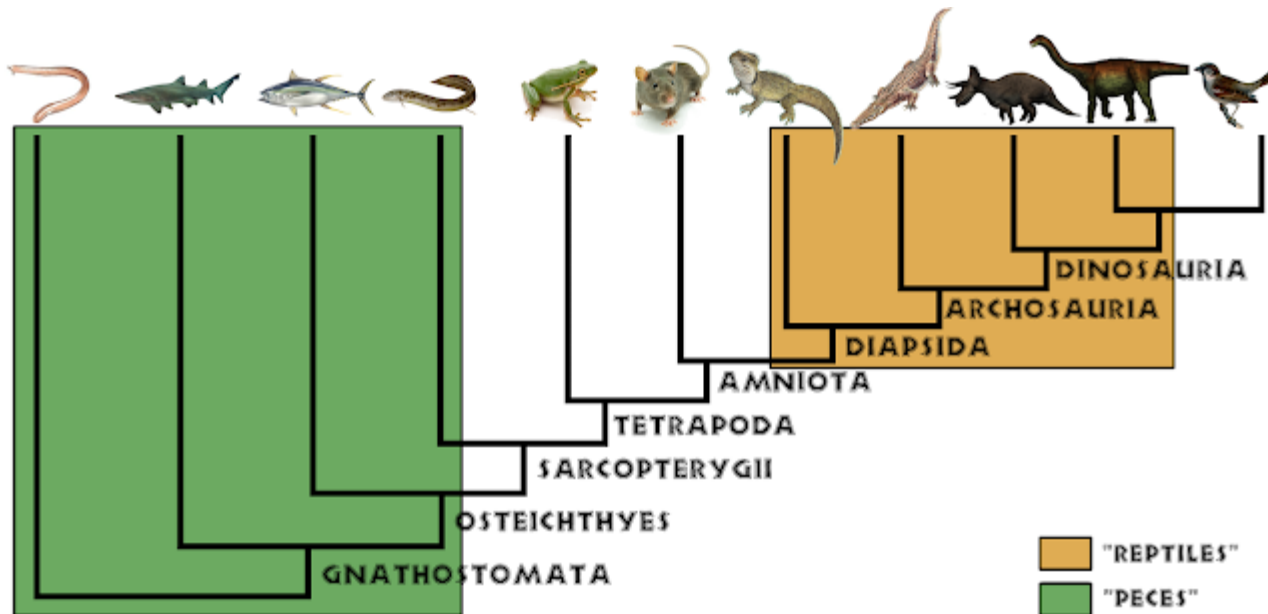
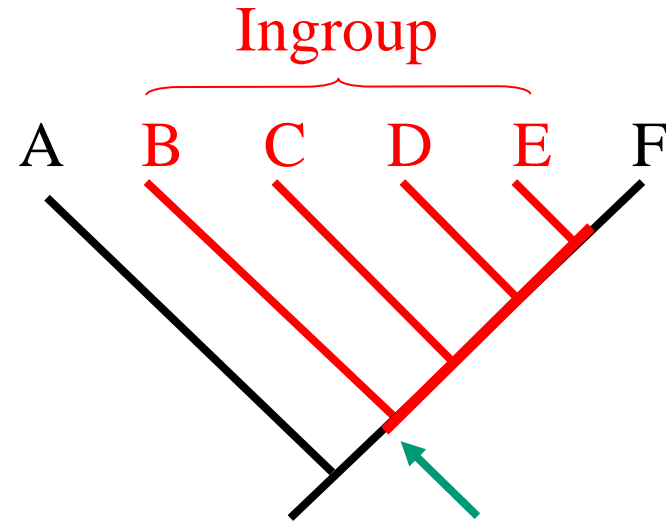
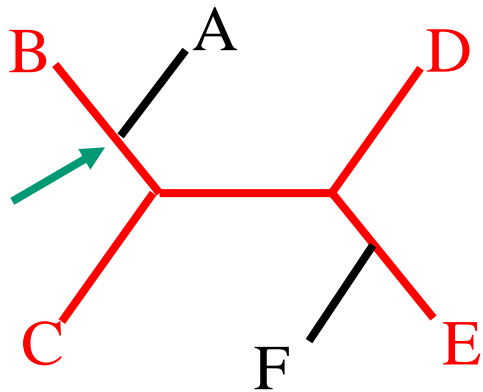


Fig. 2 Maximum likelihood phylogeny for combined data. Maximum parsimony (MP) and maximum likelihood (ML) bootstrap values as well as Bayesian posterior probabilities (BPP) are indicated. Clade names are shown on the right. Photo by T. Gamble.

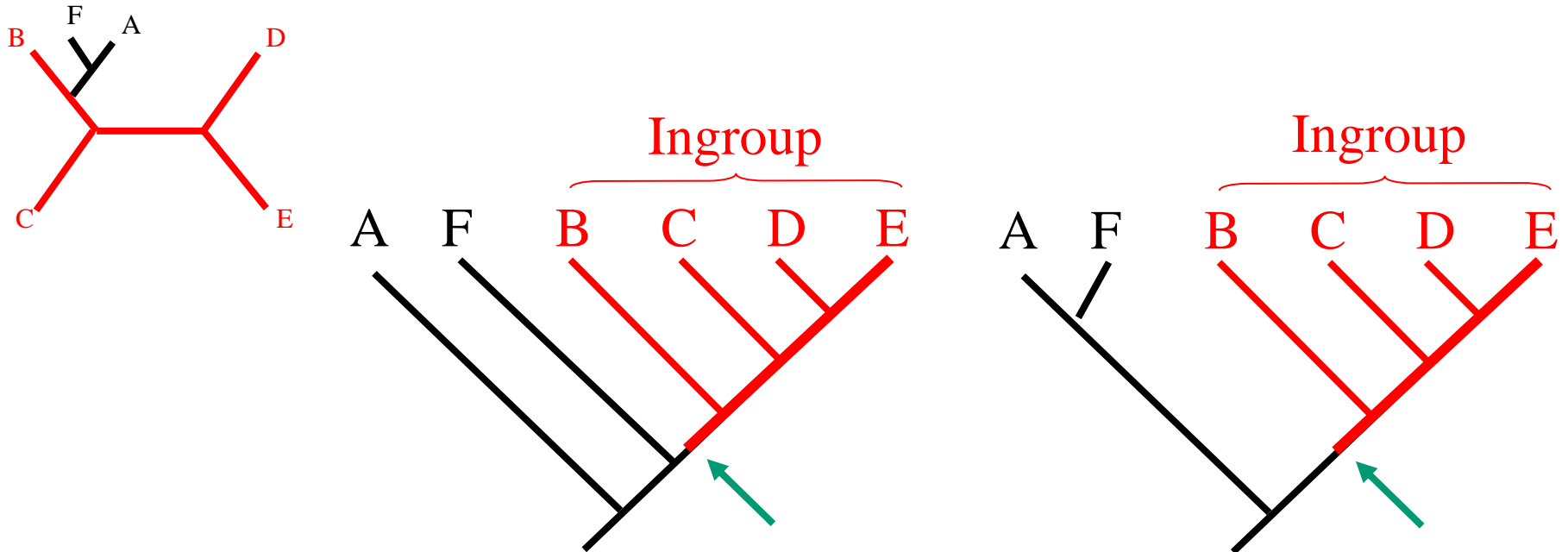
Paraphyletic ingroup



OUTGROUP: function

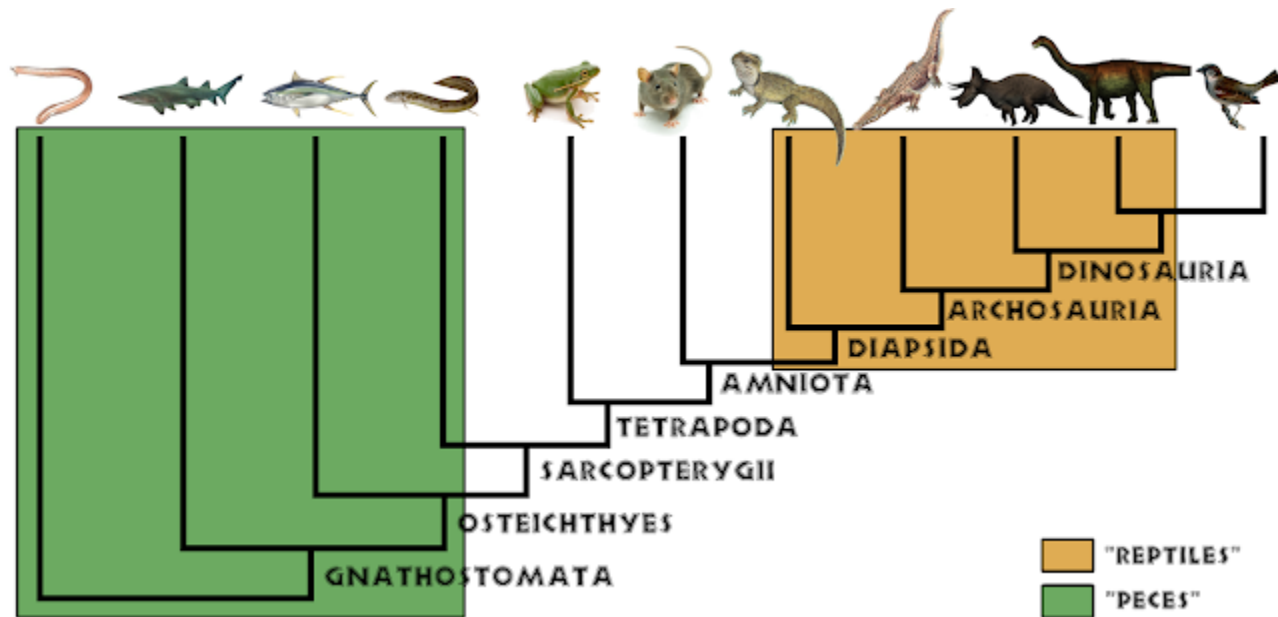
If in the analyses more than one taxon is used as outgroup, the tree will be arbitrarily rooted between one of them and the ingroup (this is what I call the functional outgroup)

If the ingroup is corroborated as monophyletic, the rooting decision (merely a graphic decision) will not impact the conclusion of monophyly of the ingroup, but it can impact the conclusion about the sister relationships



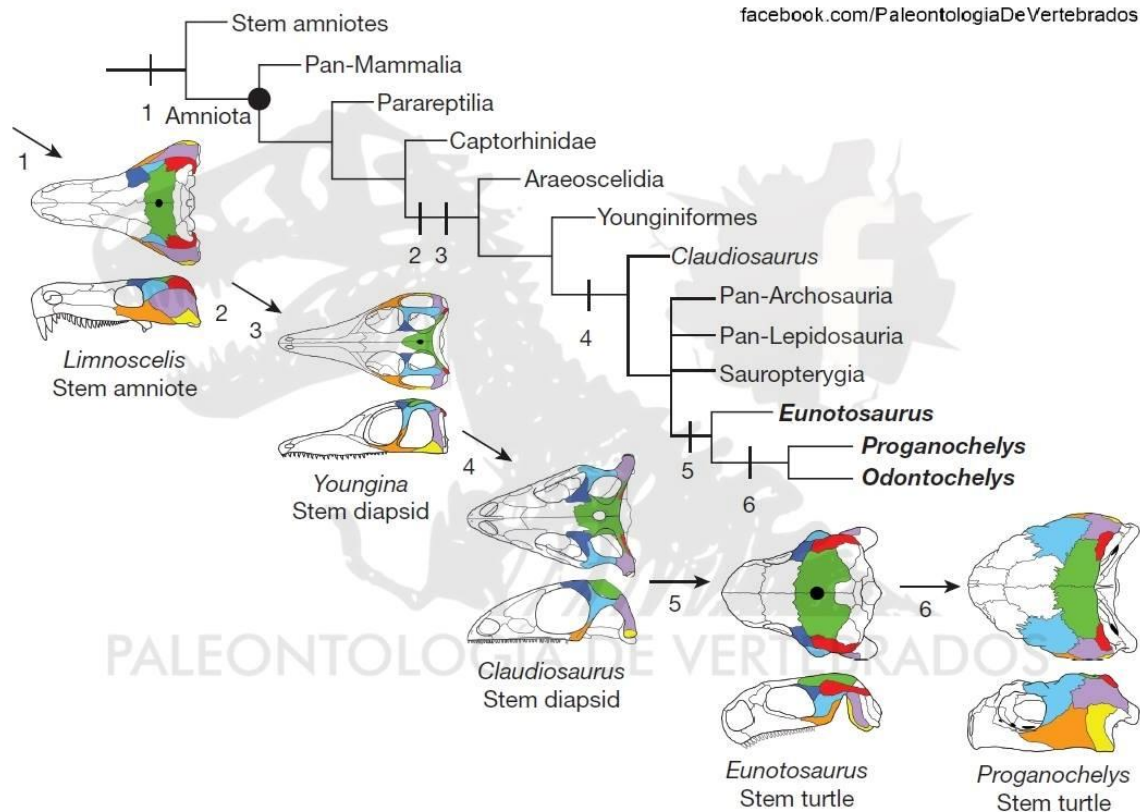
OUTGROUP

So, when more than one taxon is used as an outgroup, the one that serves as rooting reference has to be chosen arbitrarily, but not necessarily unjustifiably: it should be the theoretically most distantly related taxon

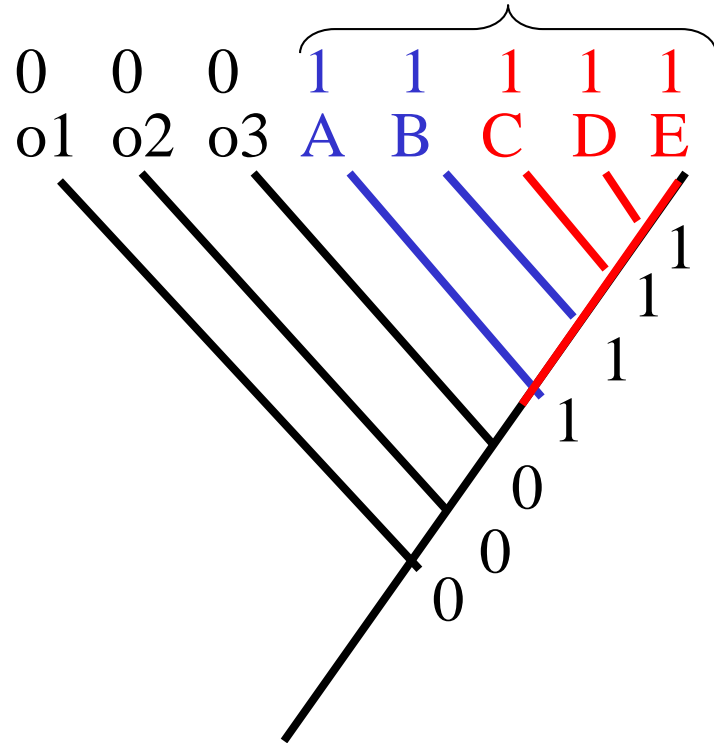


OUTGROUP: character polarity

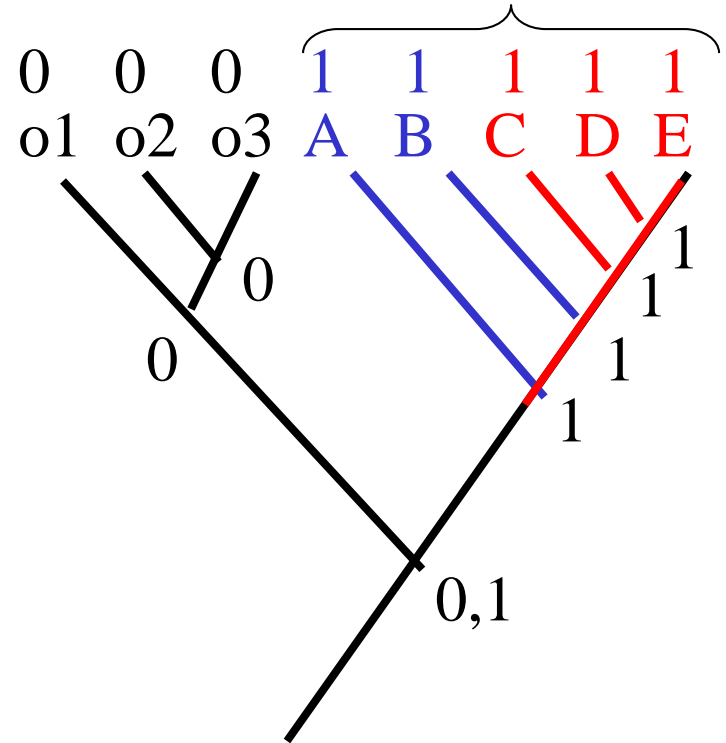
Also the interpretation of character evolution can change depending on the orientation of the tree (on the relative position of the out group)



OUTGROUPS: character polarity



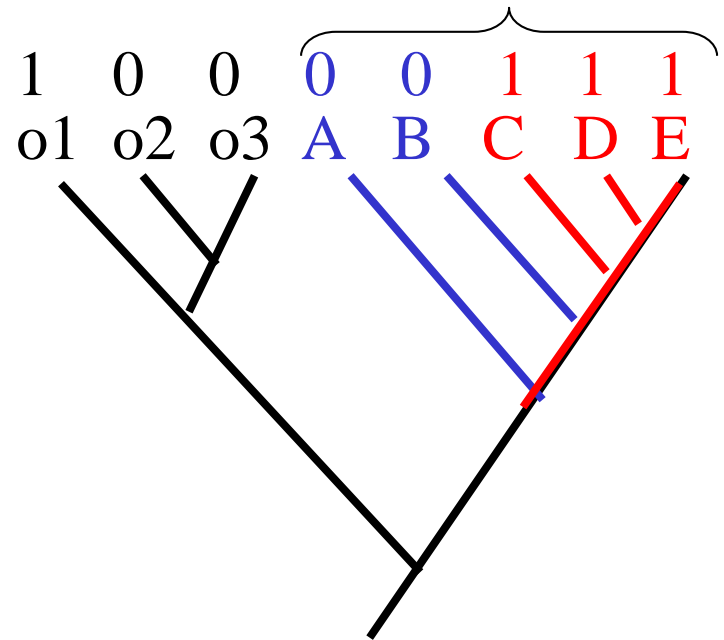
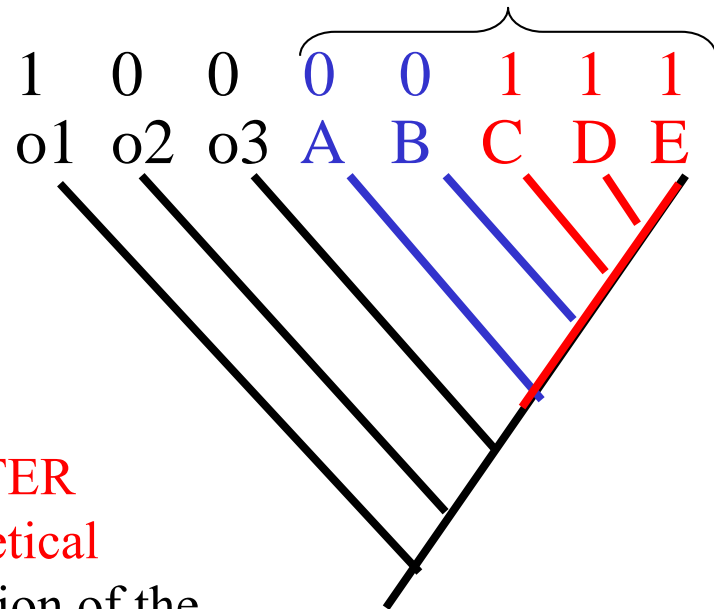
The ancestral character state for the ingroup would be interpreted to be 0



The ancestral character state for the ingroup could be either 0 or 1

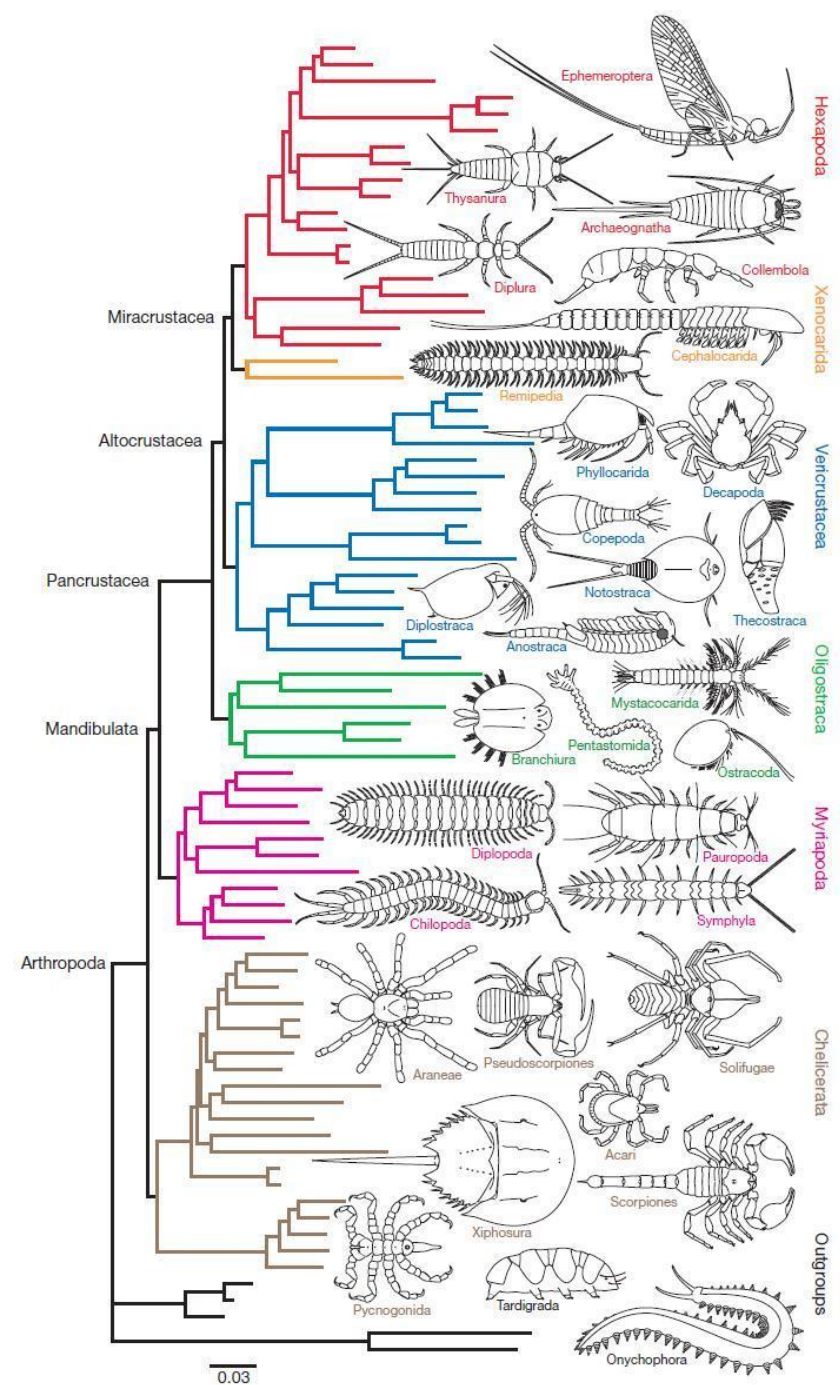
OUTGROUP: selection and graphic representation

A diverse sampling of the outgroup generally results in a paraphyletic group, with a gradient from the ingroup to a more distantly related taxon the functions to root the tree



OUTGROUP: monophyly

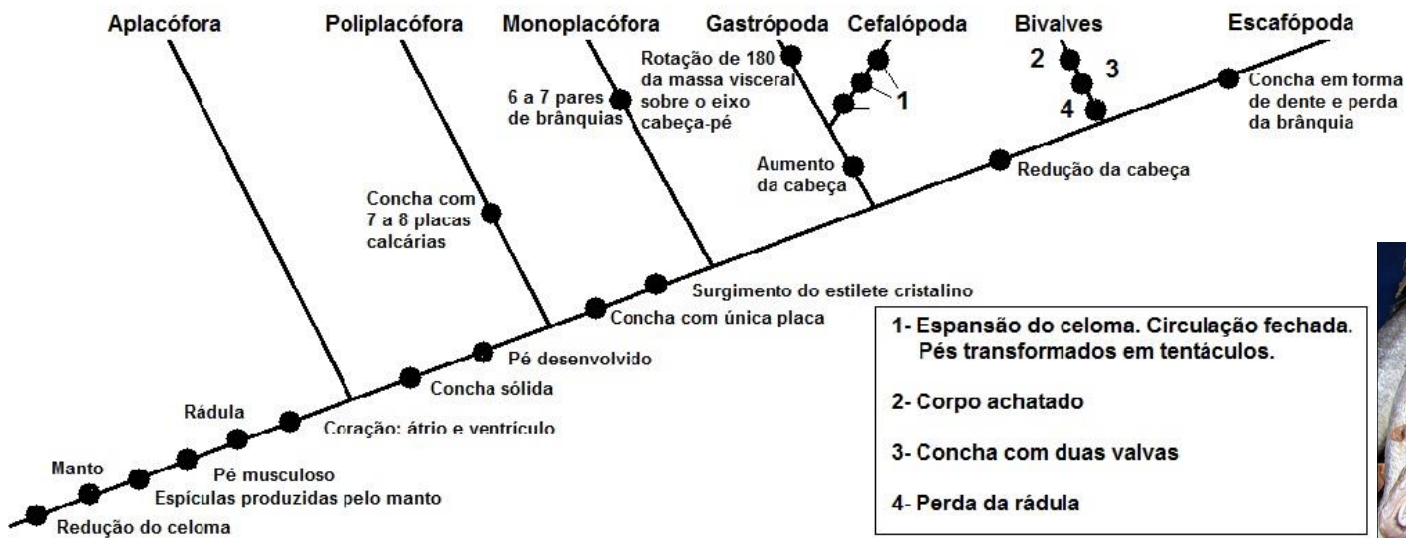
The more diverse the
representation of taxa
(outgroup and ingroup) the
more rigor in the monophyly
test for the ingroup and the
groups inside it



OUTGROUP: selection

There is no universal rule to appropriately select the outgroup because this depends upon each group, including type and quantity required to produce stable results

The best way to design the sampling of appropriate outgroups is to postulate hypothetical SINAPOMORPHIES that are shared by the members of the ingroup (character states present in the ingroup and absent in the outgroup) plus hypothetical synapomorphies shared by the ingroup and some of the outgroup members, in such a way that there is a theoretical hierarchy of synapomorphies and terminals



OUTGROUP: selection

For a good design of outgroup sampling one can use as preliminary information CLASSIFICATIONS, PREVIOUS ANALISES, or PUTATIVE SINAPOMORPHIES that can be postulated according to the hypothesis of monophyly of the ingroup

It is very important to *a priori* select one terminal as the one that unequivocally is the most distantly related and that will serve to root the tree



<https://es.wikipedia.org/wiki/Parides>

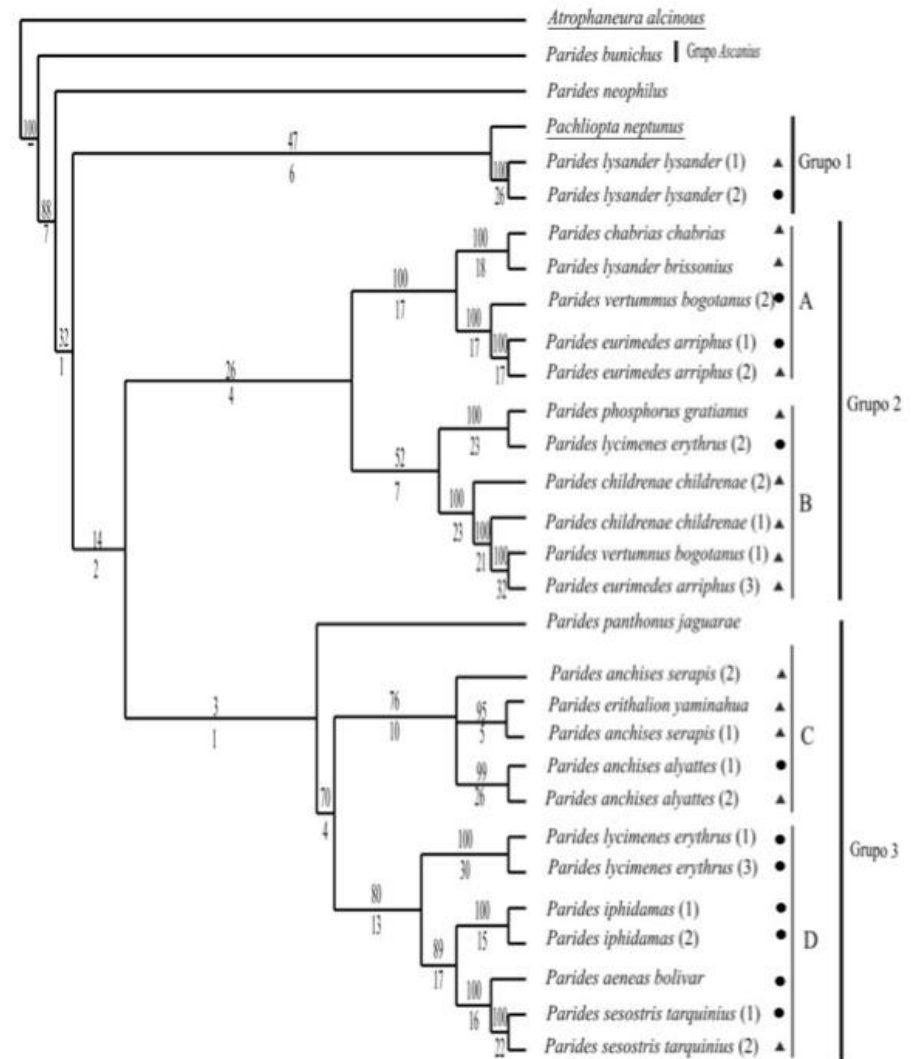


Figura 3. Árbol filogenético según análisis Bayesiano. Los valores de las ramas indican la probabilidad posterior Bayesiana. Las especies del grupo externo se muestran subrayadas.

TERMINAL SAMPLING

There is no rule to predict how many terminals fulfil the requirements for the interpretation of a tree as a phylogeny and for the correct retrieval of natural relationships

The objective is to obtain results that reflect phylogenetic relationships that we believe are natural and that the results are stable

For that, it is desirable to include in a phylogenetic analysis as much comparative information as possible depending upon availability (at the level of terminals, but also characters)

CLADISTICS	
Study units (terminals)	Populations (becoming more common), species or higher hierarchical levels (genera, family, etc.)
Number of characters	As many as possible
Type of characters	Qualitative and/or Quantitative (now possible)
Similitud	Special: reflecting common ancestor (homology)
Method	Parsimony (not assuming more explanations than those that are strictly necessary to explain the observations) or probabilistic (applyin evolutionary models)
Importance of the degree if diversification	Irrelevant
Evolutionary interpretation	Not necessary
Main component in evolution	Cladogenesis
Ancestors	Hypothetic
Homology	Hypothesizd to begin (Primary) followed by a test
Diagram	Cladogram or phylogram (with branch lenghts)
Direction of evolutionary changes	<i>A posteriori</i>
Groups accepted in the clasification	Monophyletic
Non inheritable features (e.g., geography)	<i>A posteriori</i>