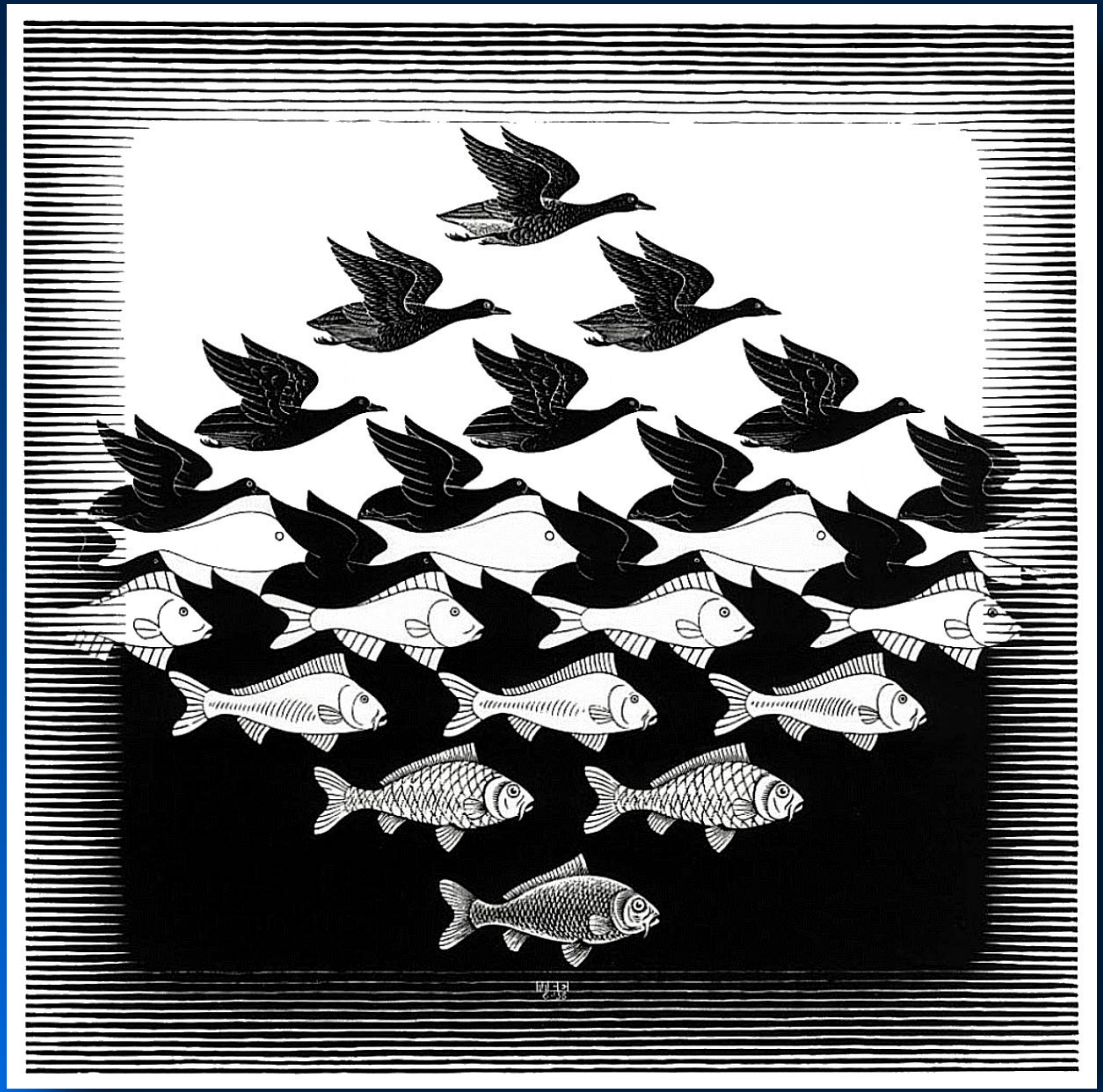
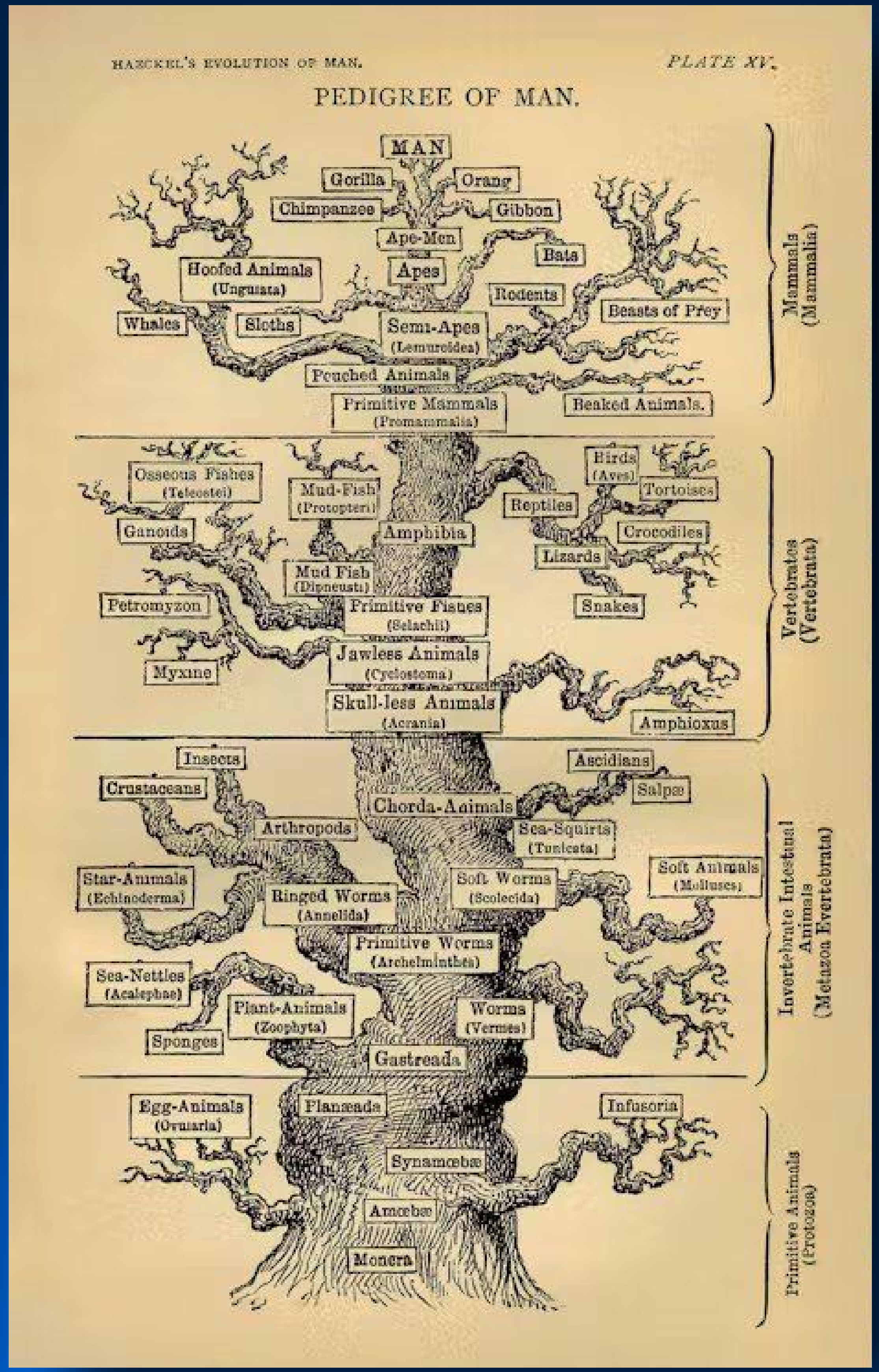
NJU Course

Principles of Paleobiology

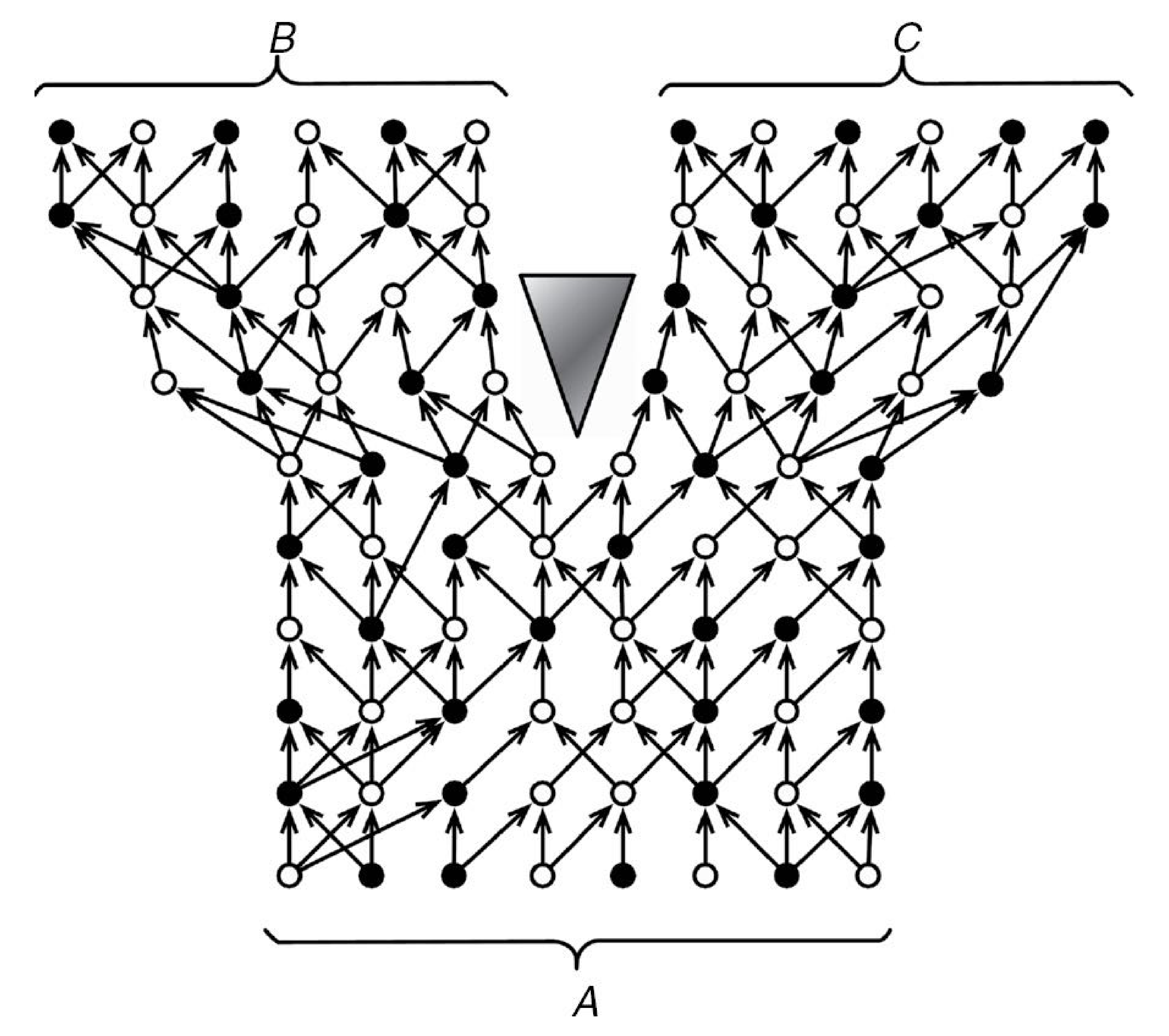
Phylogenetic Inference, Cladistics & Phylogeny



Sky and Water (M. C. Escher, 1938)



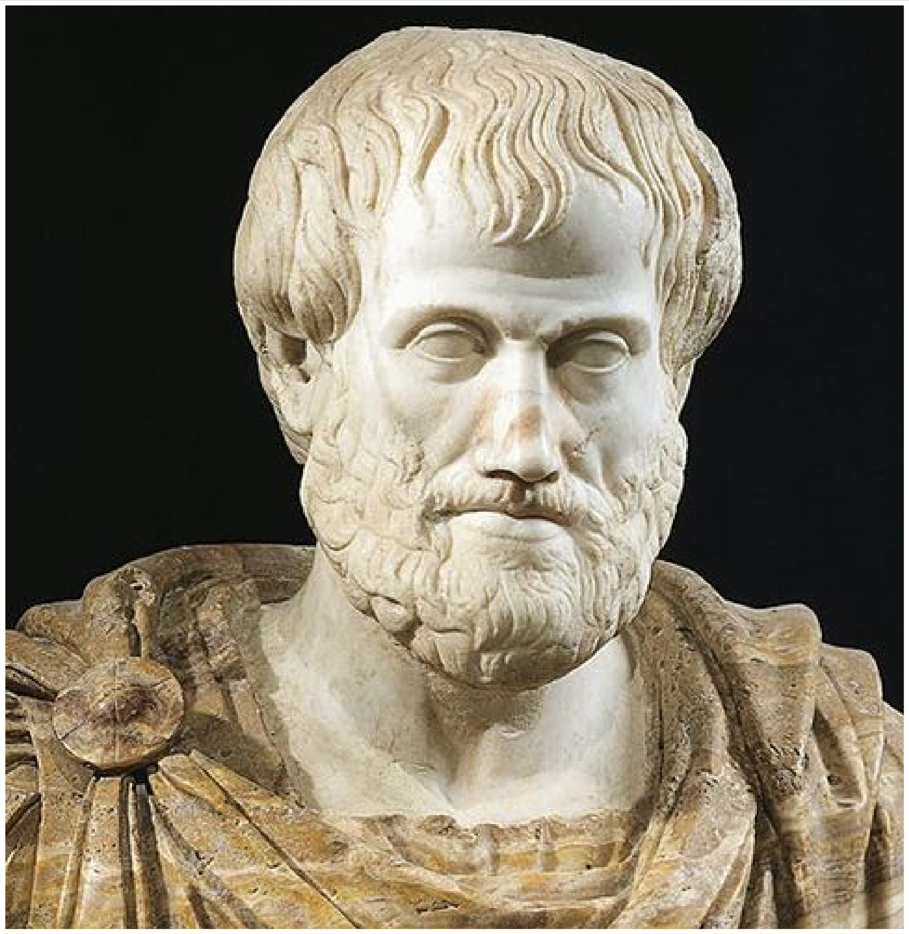
Haeckel (1866)



Hennig (1966)

Phylogenetics, Cladistics & Phylogeny

The Founders of Evolutionary Theory

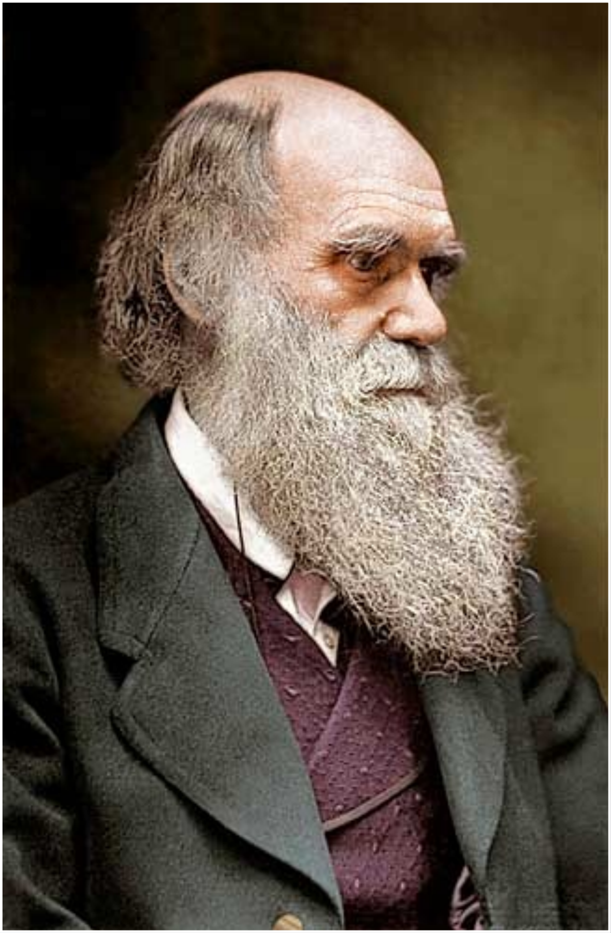


Aristotle
(384 – 322 BC)

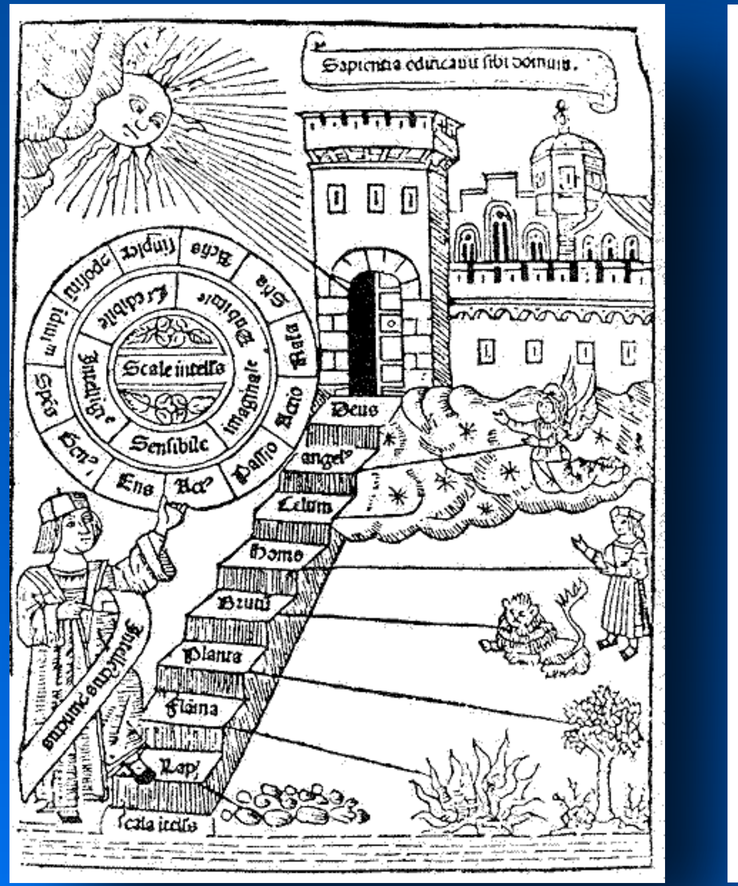
Pierre Louis Maupertuis
(1698 – 1759)

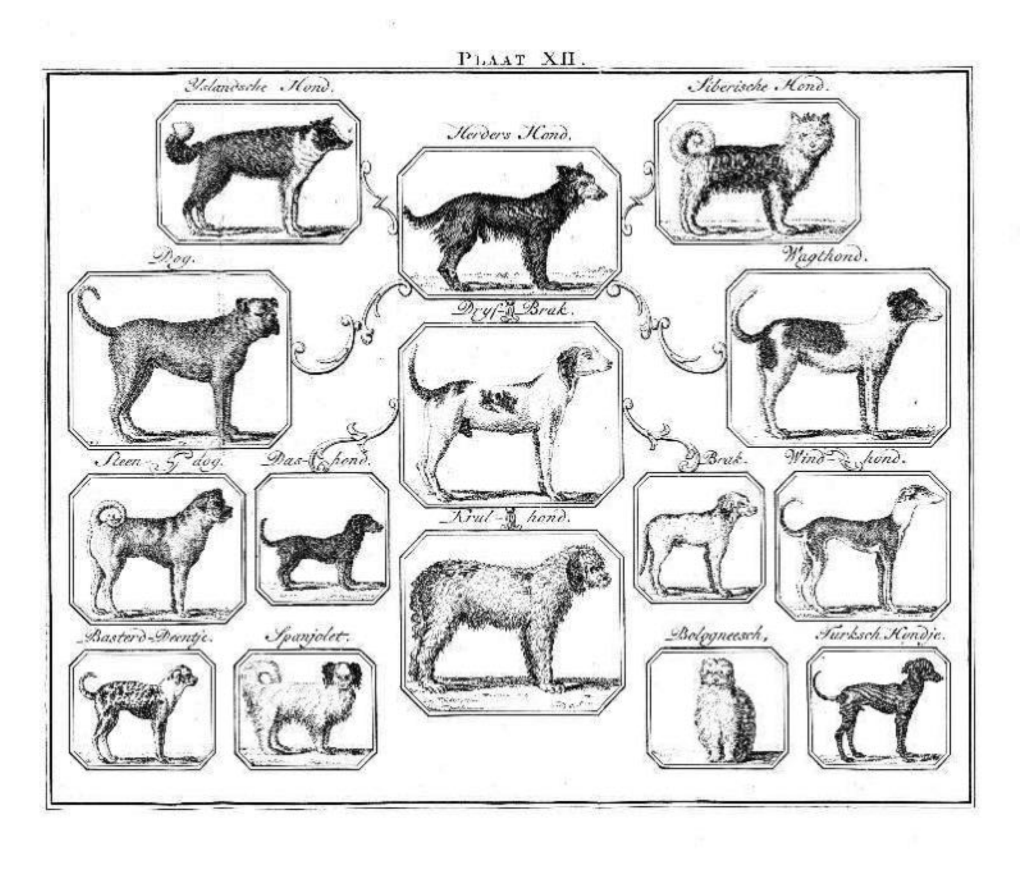
Georges-Louis Leclerc, Comte de Buffon
(1707–1788)

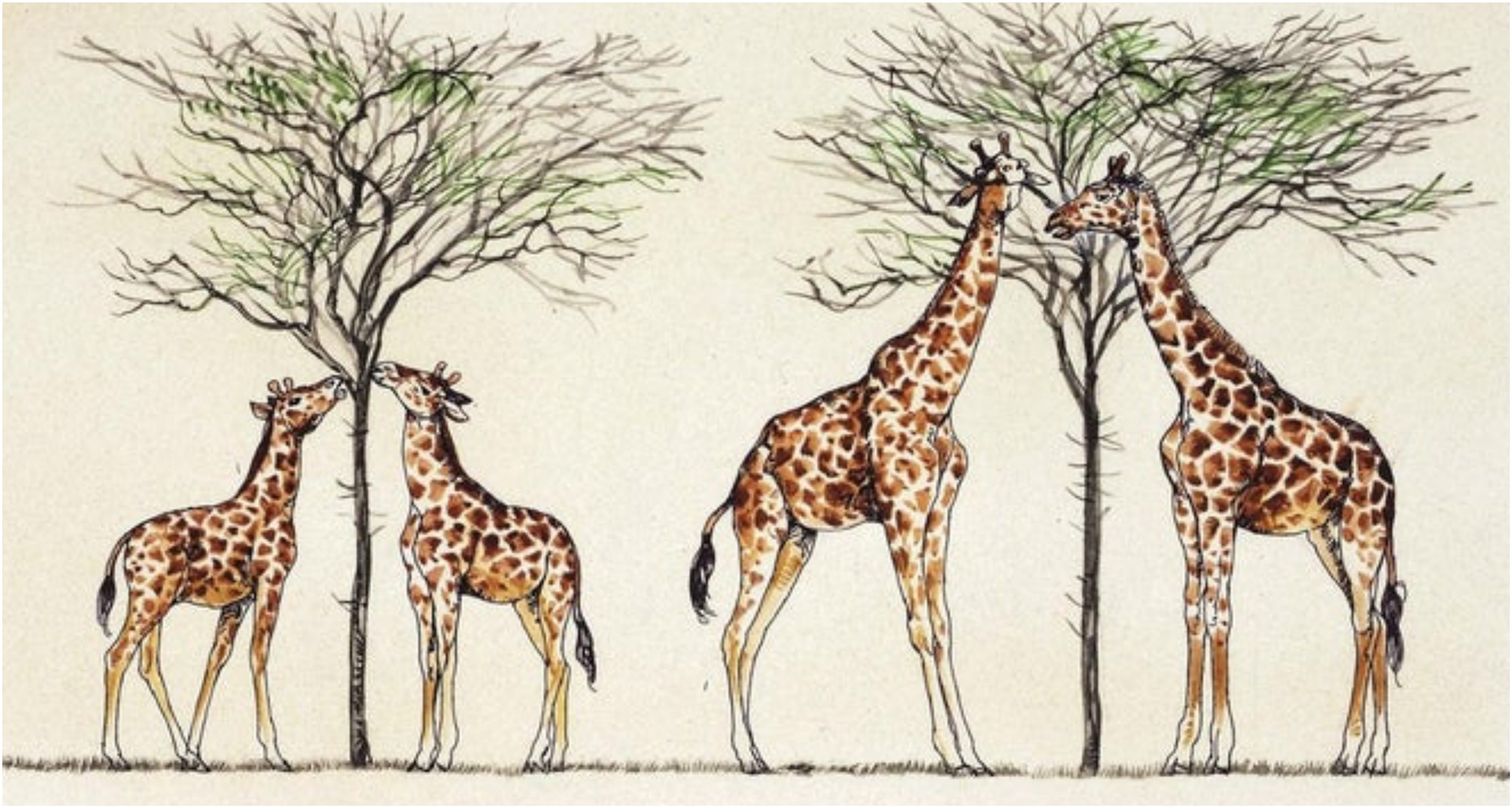
Jean-Baptiste Lamarck
(1724 – 1829)

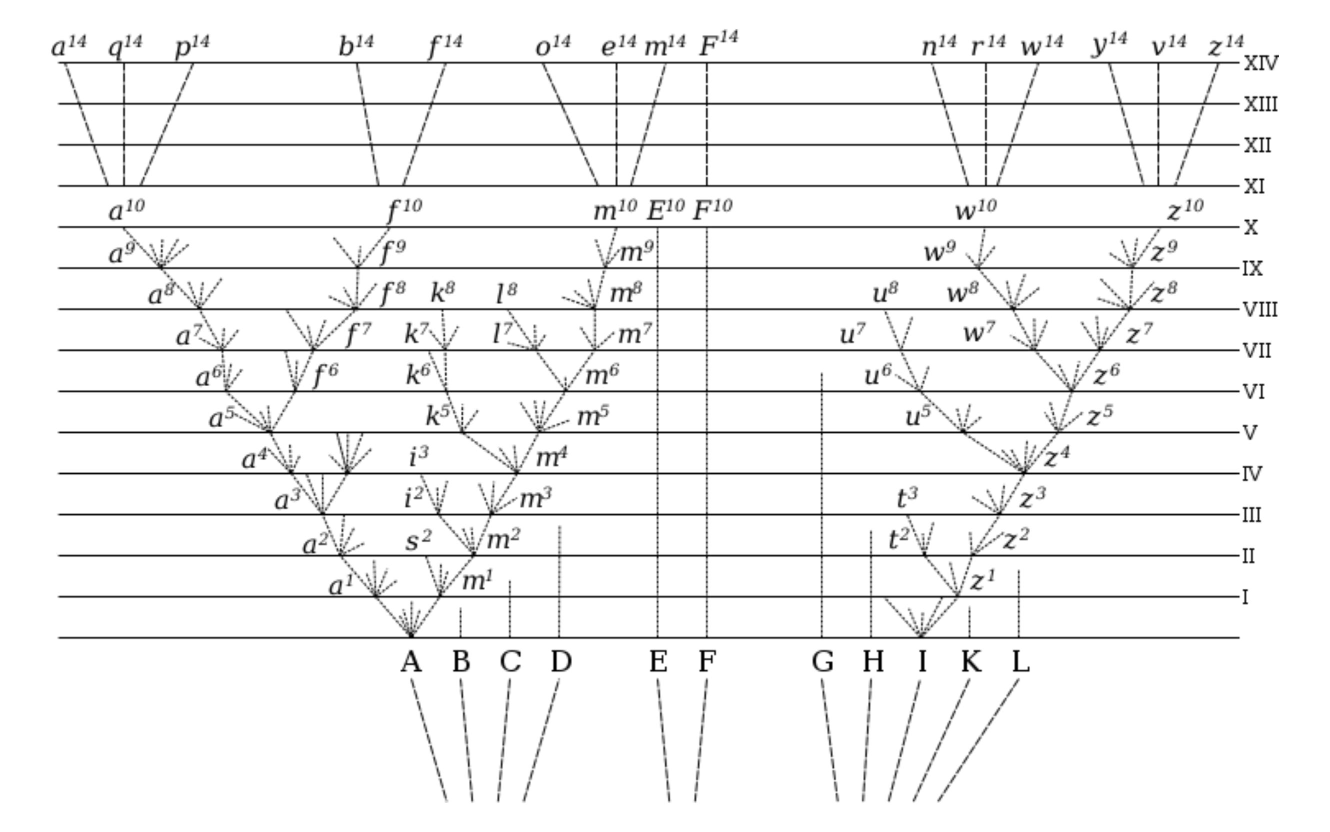


Charles Darwin
(1809 – 1882)





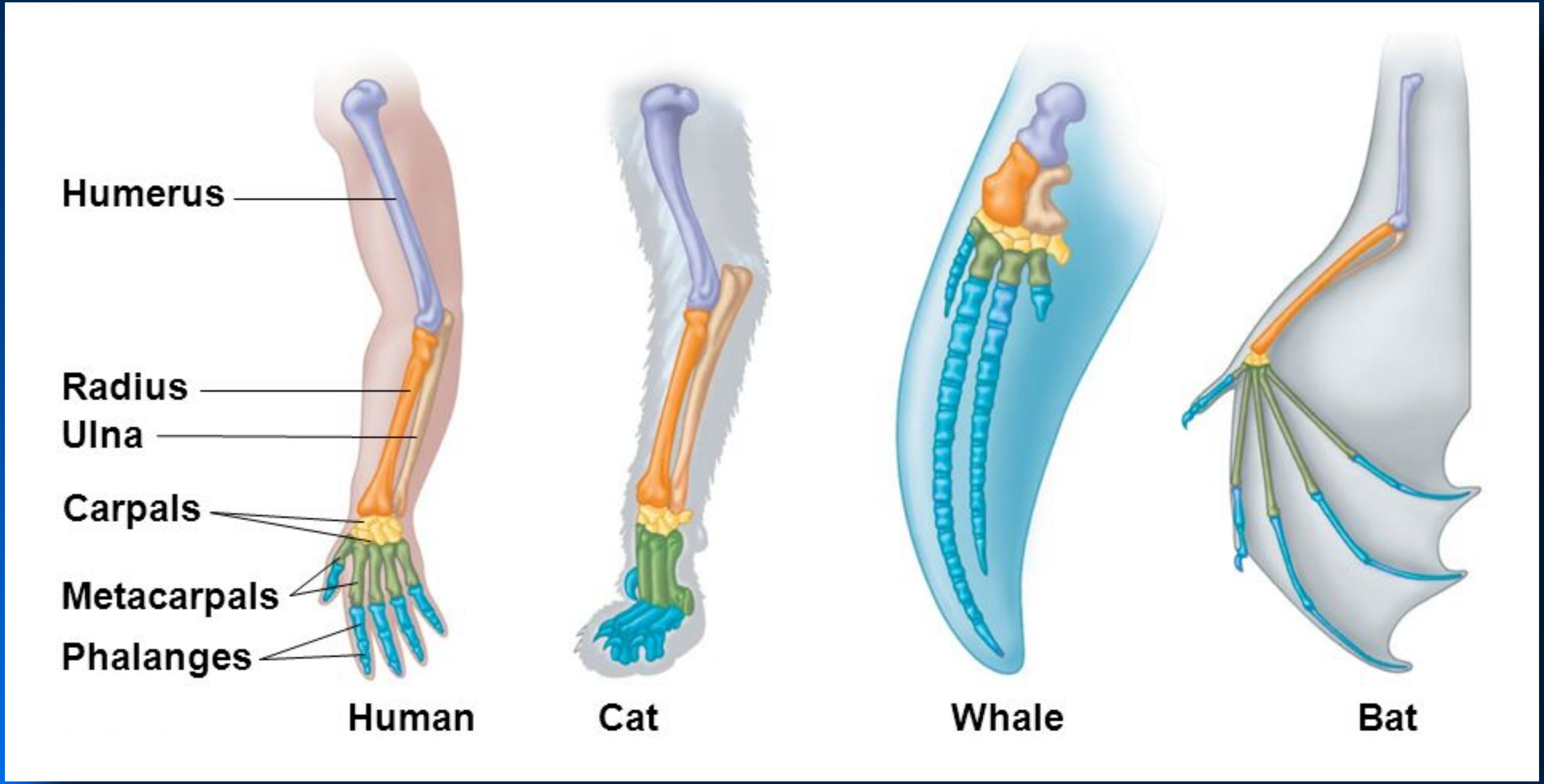




Phylogenetics, Cladistics & Phylogeny

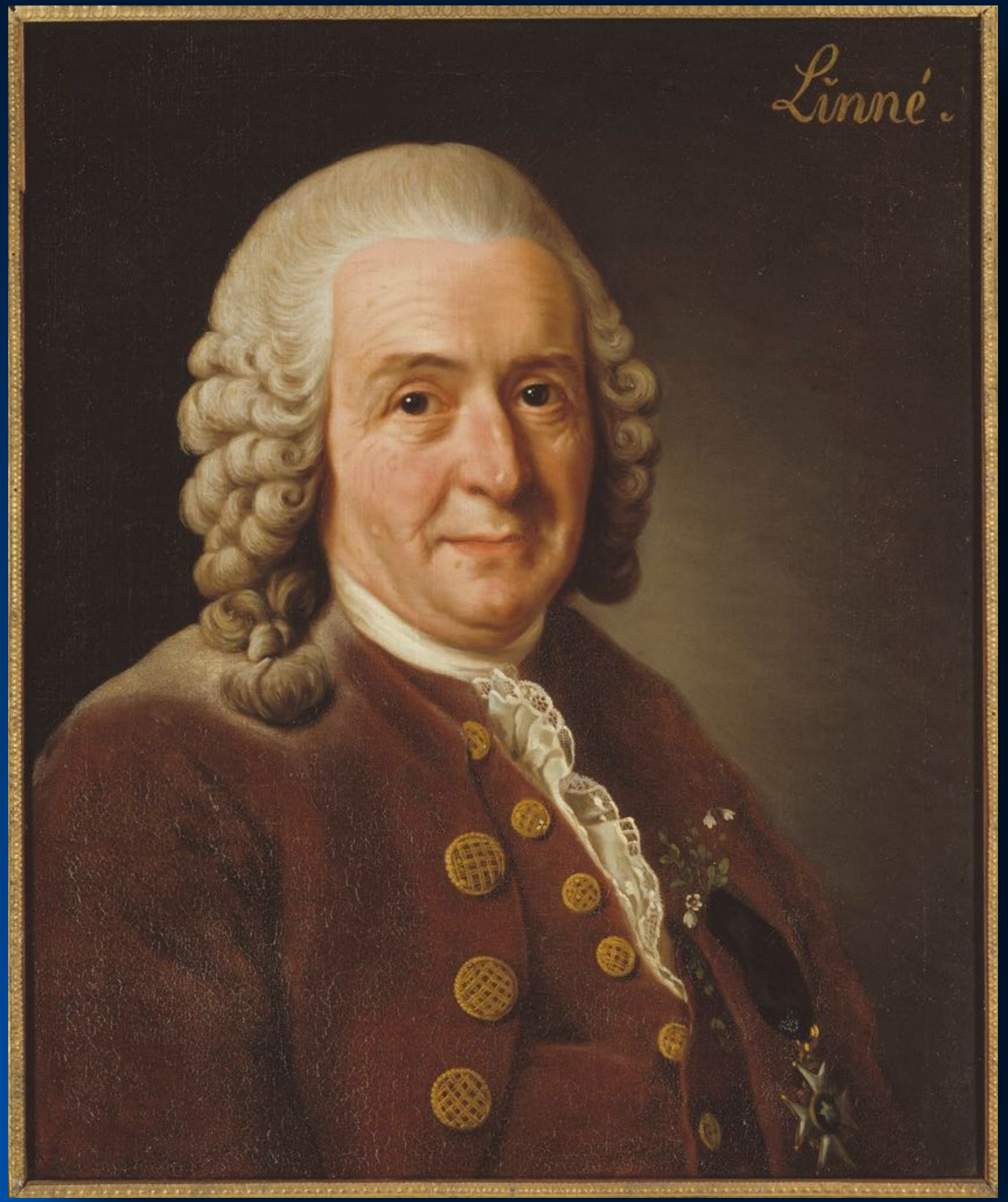
Evidence for Evolution: Homology

Similarity in the forms, positions, and developmental sequences of structural components in different species due to shared ancestry.



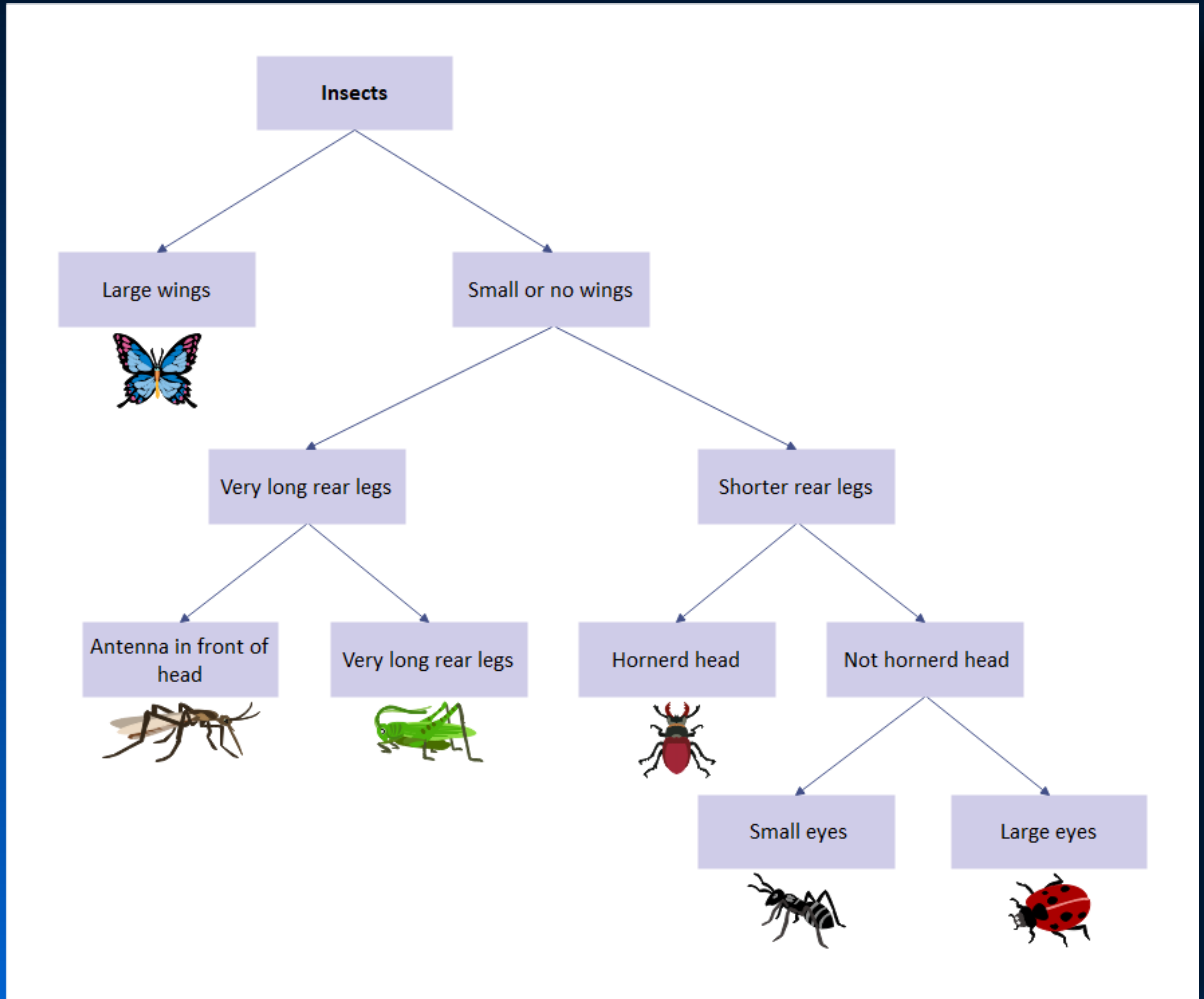
Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Classification



Carlos Linnaeus
(1707 – 1778)

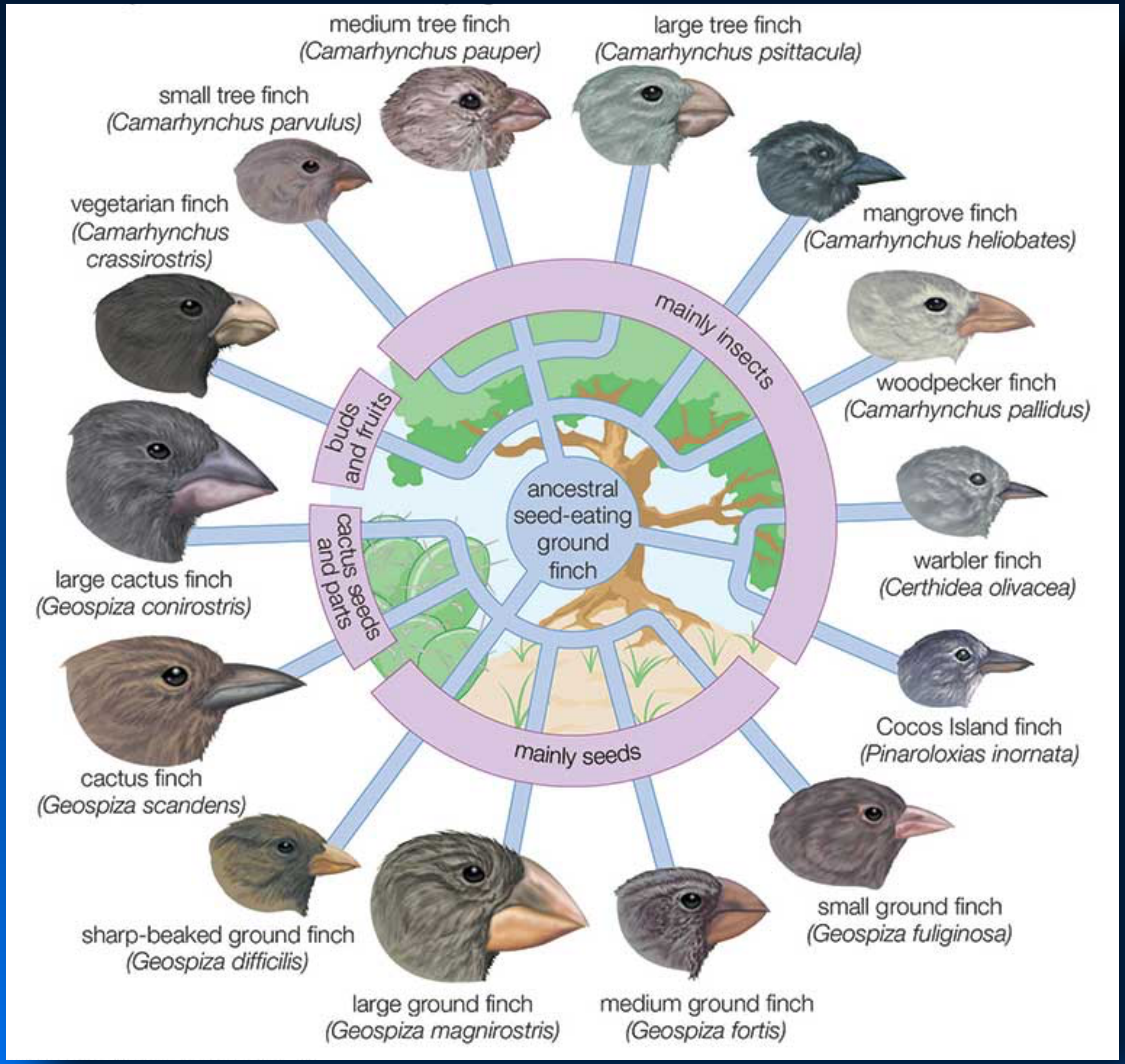
Linnaeus observed that the distribution of morphological characteristics in many species follow a hierarchical pattern of distribution. The existence of this pattern is why the Linnean system of classification is hierarchical. Later, it was realized this pattern is consistent with the concept of descent with modification (= evolution).



- **Insects**
  - Large wings
  - Small or no wings
    - Very long rear legs
      - Antenna in front of head
      - Very long rear legs
    - Shorter rear legs
      - Hornerd head
      - Not hornerd head
        - Small eyes
        - Large eyes

Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Adaptation



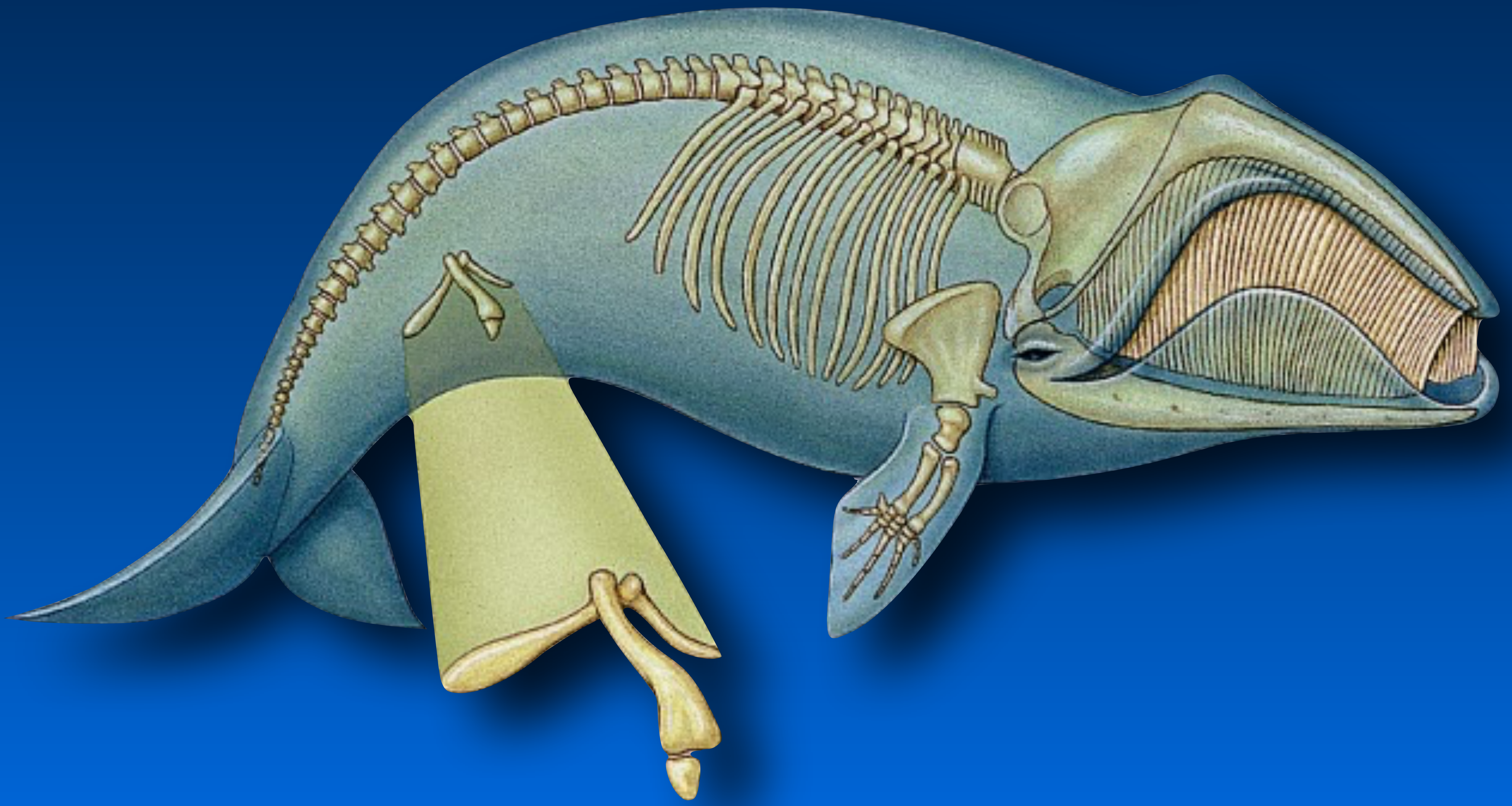
In many groups of morphologically similar species details of the variation exhibited by structures critical to their survival exhibit patterns of similarity and difference that suggest the structures have been optimized to perform specific functions relative to the characteristics of the environments in which each species occurs.

Note, direct adaptive use does not explain all aspects of organismal morphology or phylogenetic history. It is tempting to ask “What is that for?” when confronted with a novel morphological feature. There are many non-directly adaptive reasons why a feature might be present. The evidence for all reasonable hypotheses of origin should be considered before offering an interpretation.

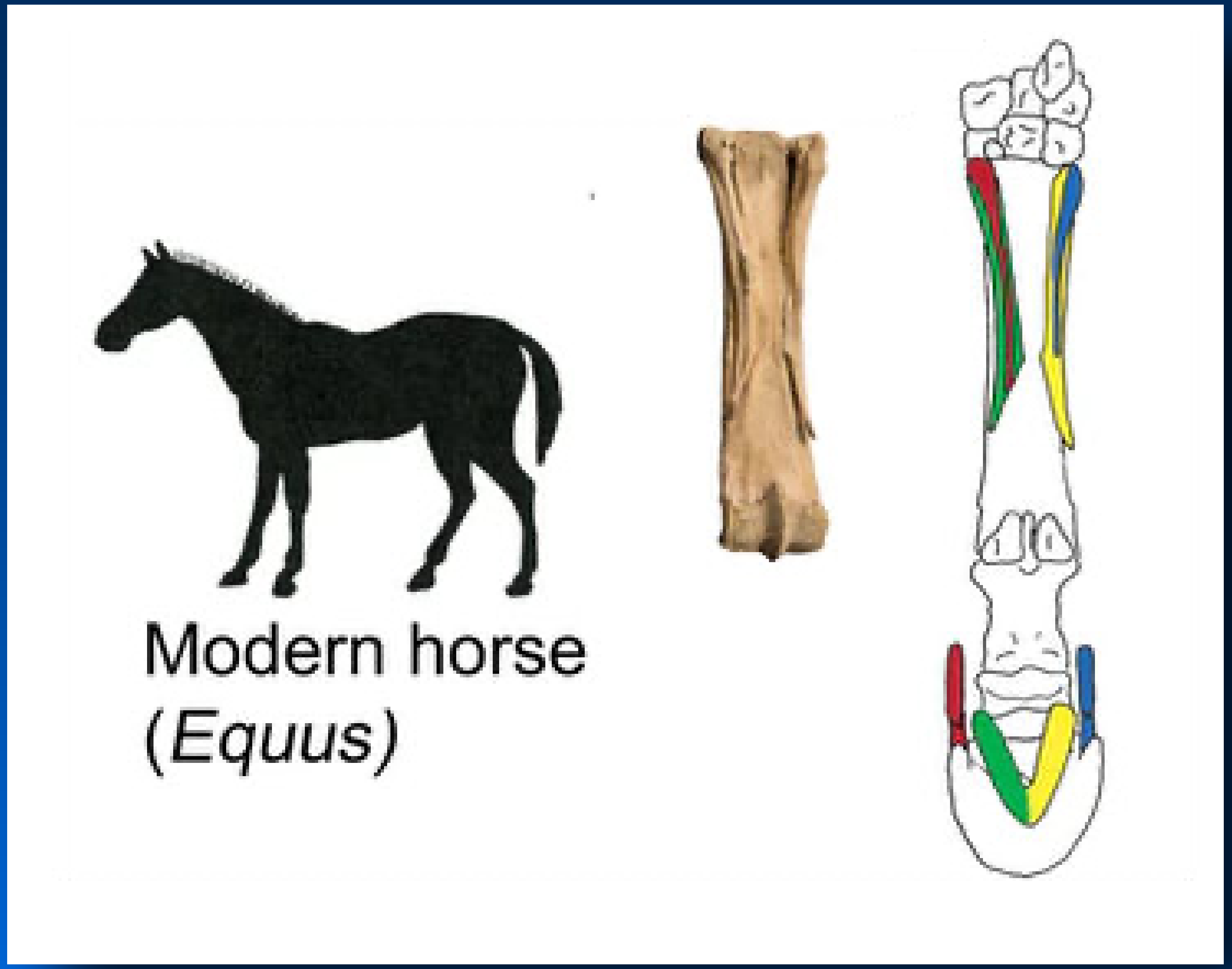
Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Vestigial Structures

An incomplete or degenerate remnant of an organ or structure in some species that functions in a normal sense and for a definite purpose in similar species. Examples include: hind limb bones in aquatic mammals, teeth in some birds, dewclaws in canids, appendix in humans.



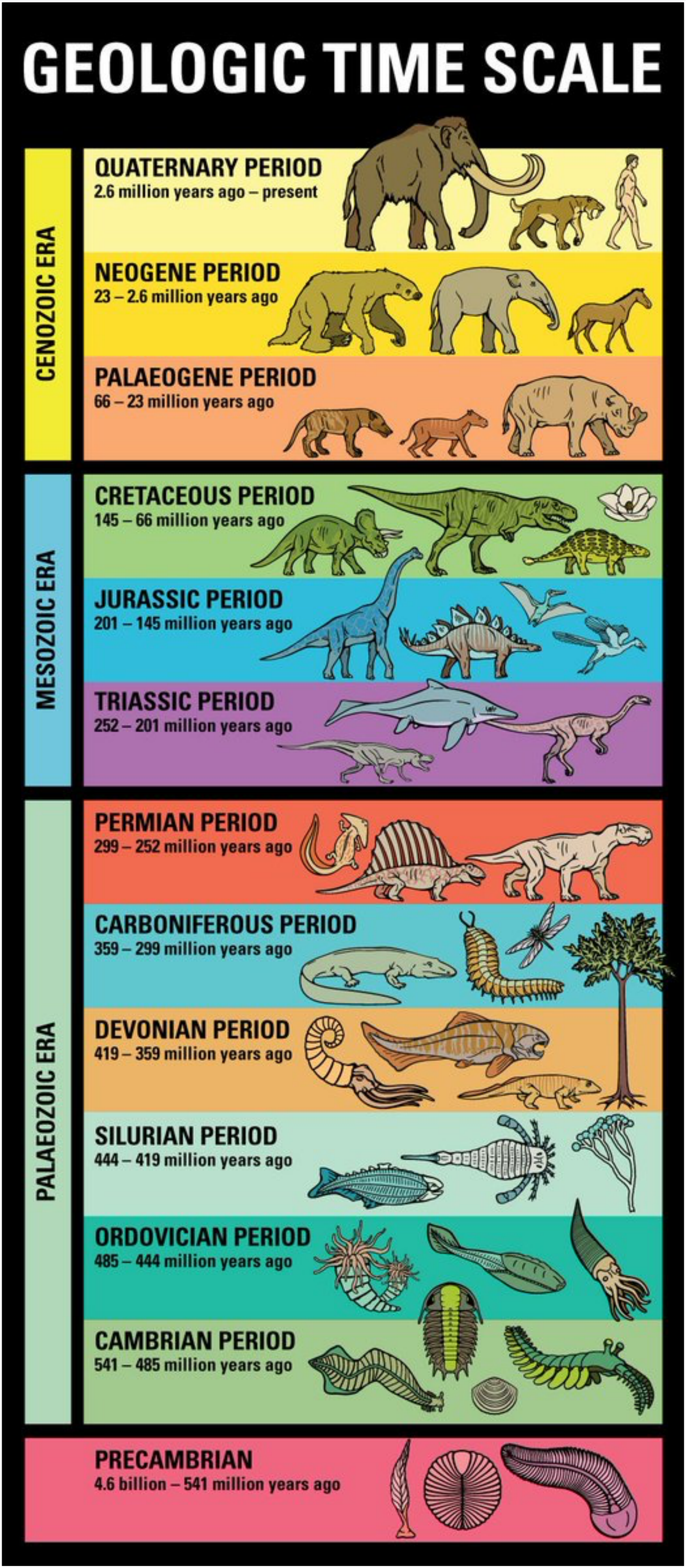
Vestigial Pelvis of Right Whale
(*Eubalaena gracilis*)



Vestigial Toes of Horse
(*Equus equus*)

Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Fossils - Biotas over Time



In the stratigraphic record the oldest sediments are characterize by fossils of small size and simple form, suggesting that the species living at that remote time were themselves small and morphologically simple.

Size and morphological complexity increase progressively in younger sediments as does the range of environments and habitats in which fossils are found.

Traditionally, this pattern was seen as evidence of a “complexifying force”. But this pattern of increasing size, complexity and ecological diversity is also compatible with the progressive adaptation of species to new environments and progressive ecological specialization.

This having been said, the apparent existence of long-term and quite consistent trends in morphological development still presents a challenge to the concept of environmentally driven morphological change via natural selection.

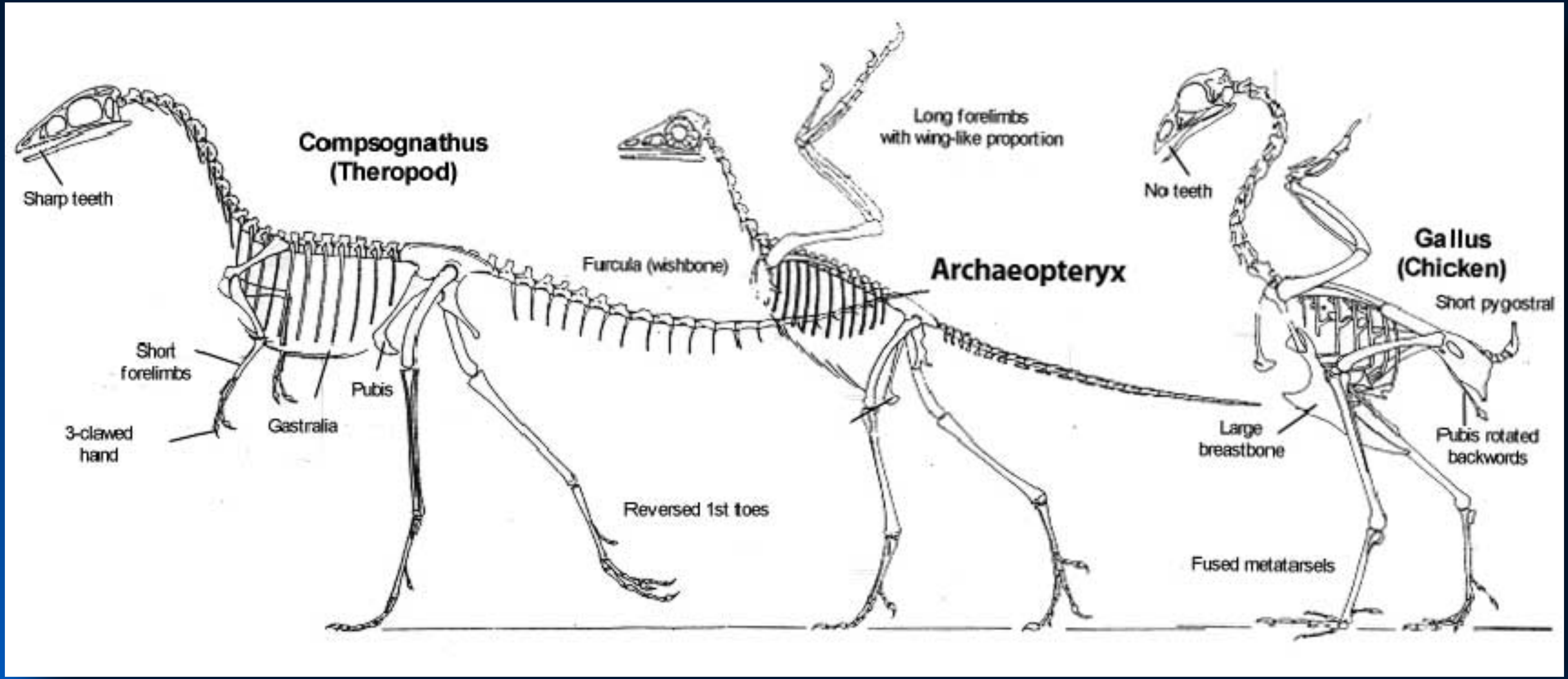
Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Existence of Intermediates

Since Darwin’s theory states that all life evolved from a single common ancestor it implies that morphological intermediates should exist between all major organismal groups. At first this was a problem because, by 1859, few truly intermediate fossil species has been found. However, in 1860 a single fossil feather was discovered in the Middle Jurassic Solenhofen limestone and, in 1861, a nearly complete specimen of an intermediate between dinosaurs and birds was found - *Archaeopteryx*.

Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Existence of Intermediates



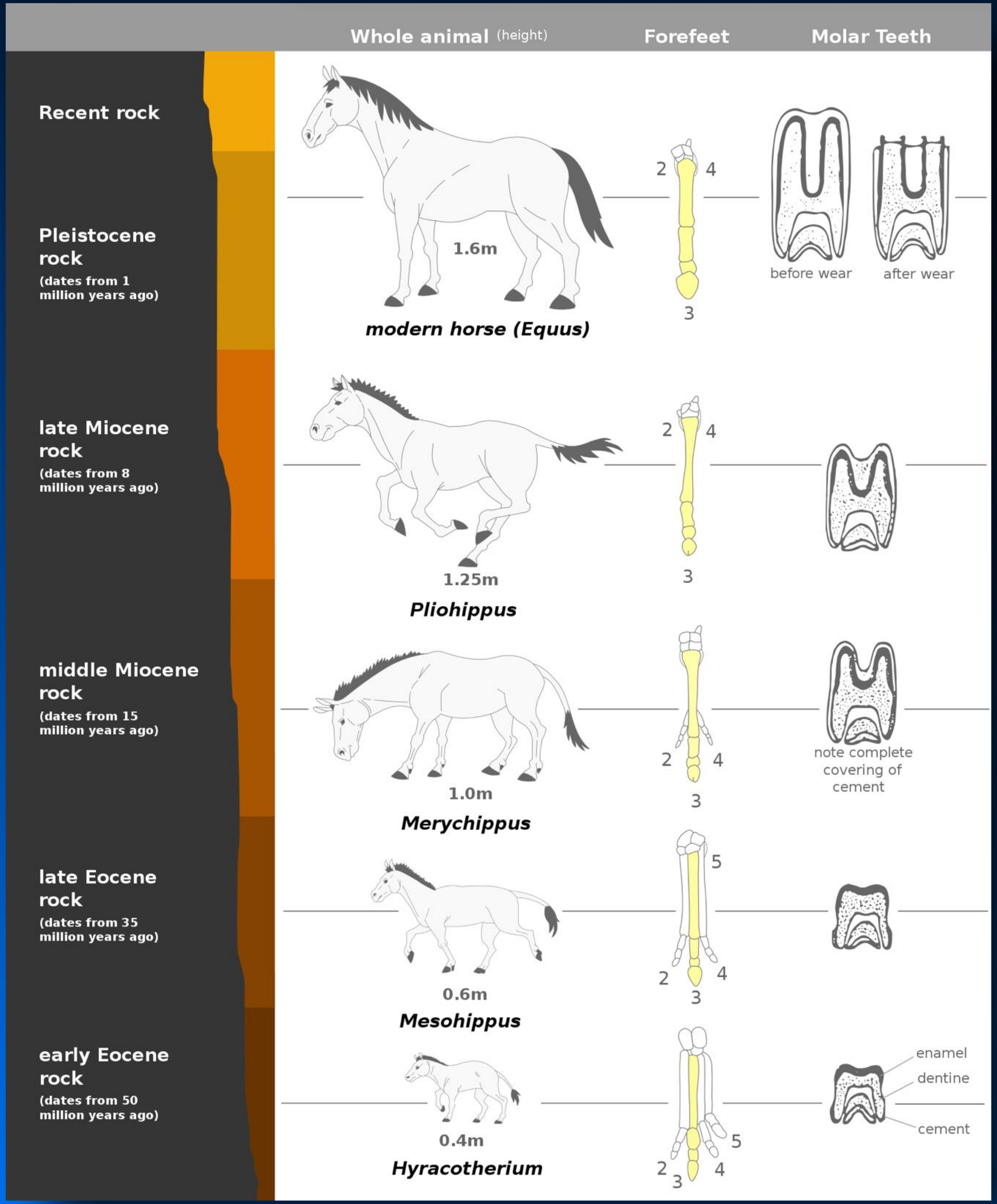
- Pubis points forwards
- Short forelimbs
- 3-clawed hand
- Separate metatarsals

- Gastralia
- Teeth
- Pubis points backwards
- Long forelimbs

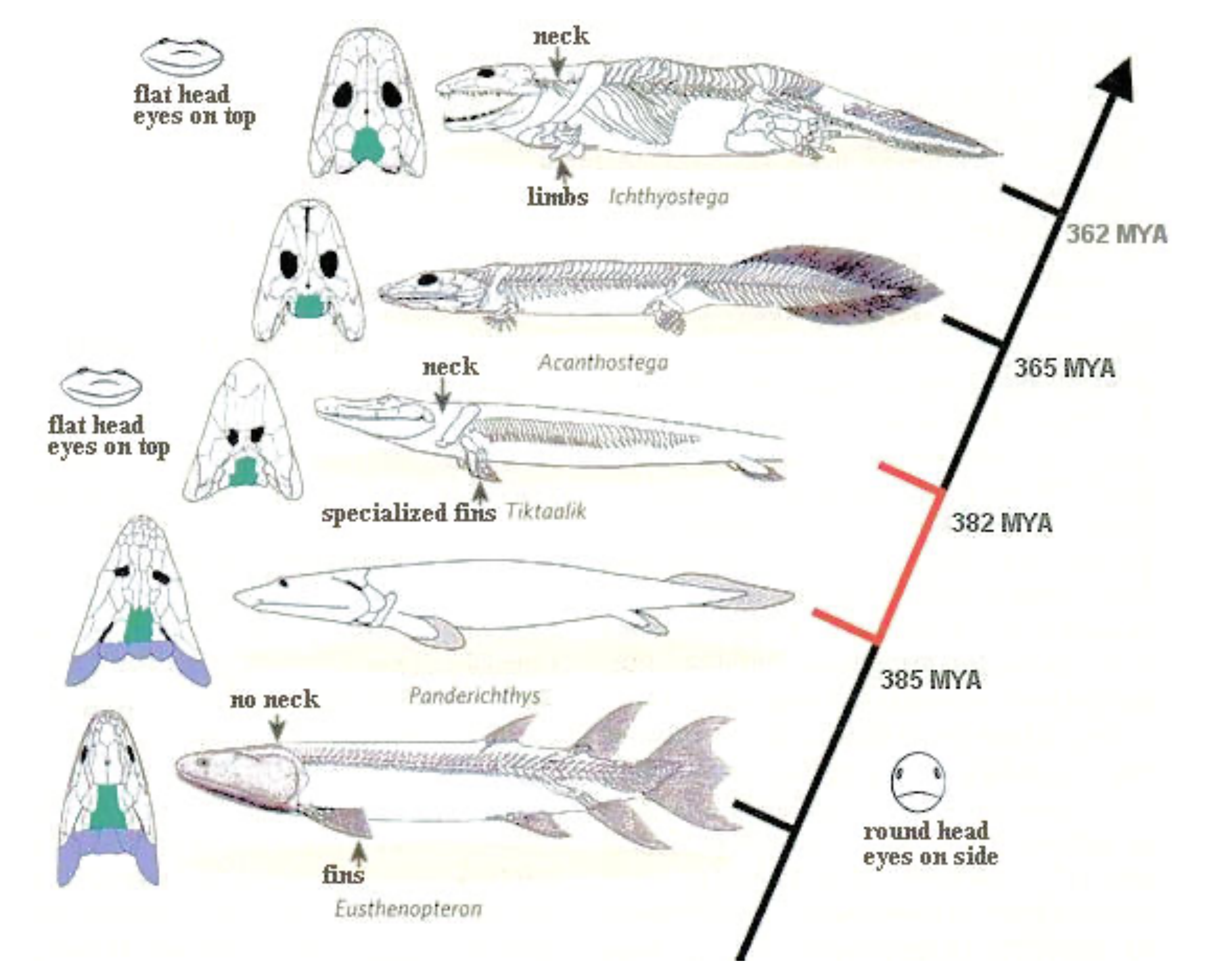
- No claws on hand
- Fused metatarsals
- Breastbone
- No Teeth

Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Existence of Intermediates



Subsequent to Darwin's time many more-or-less complete lineages of fossil species have been discovered.



Phylogenetics, Cladistics & Phylogeny

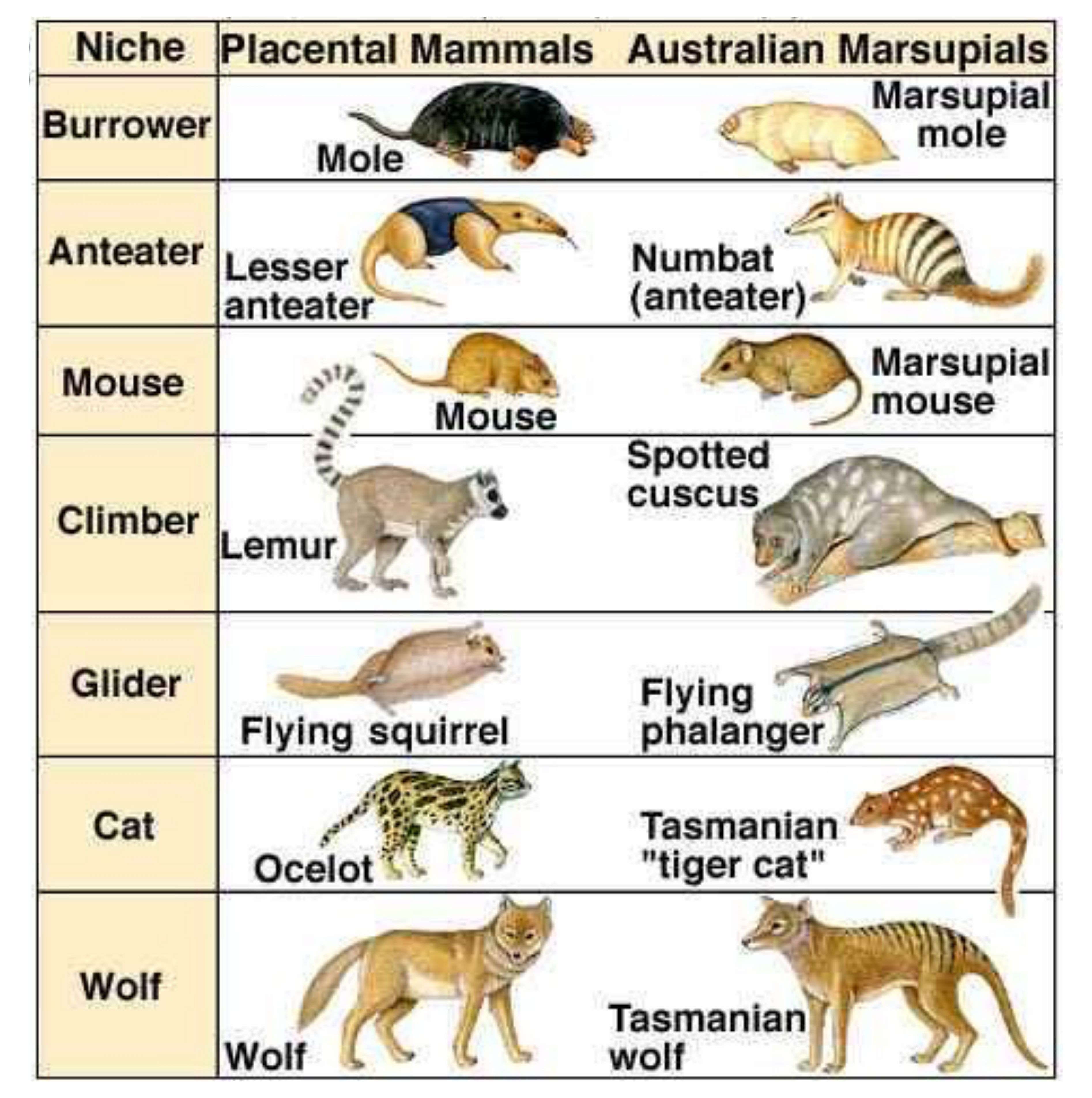
Evidence for Evolution: Biogeography

Species on different continents that live in similar environments, but that are clearly different in basic aspects of their biology nevertheless tend to exhibit many superficial similarities and resemblances.

This suggests:

- different organismal groups are not distributed uniformly over the globe;
- the problems posed by similar environments and life-styles are addressed (in many cases) in similar ways irrespective of species evolutionary histories.

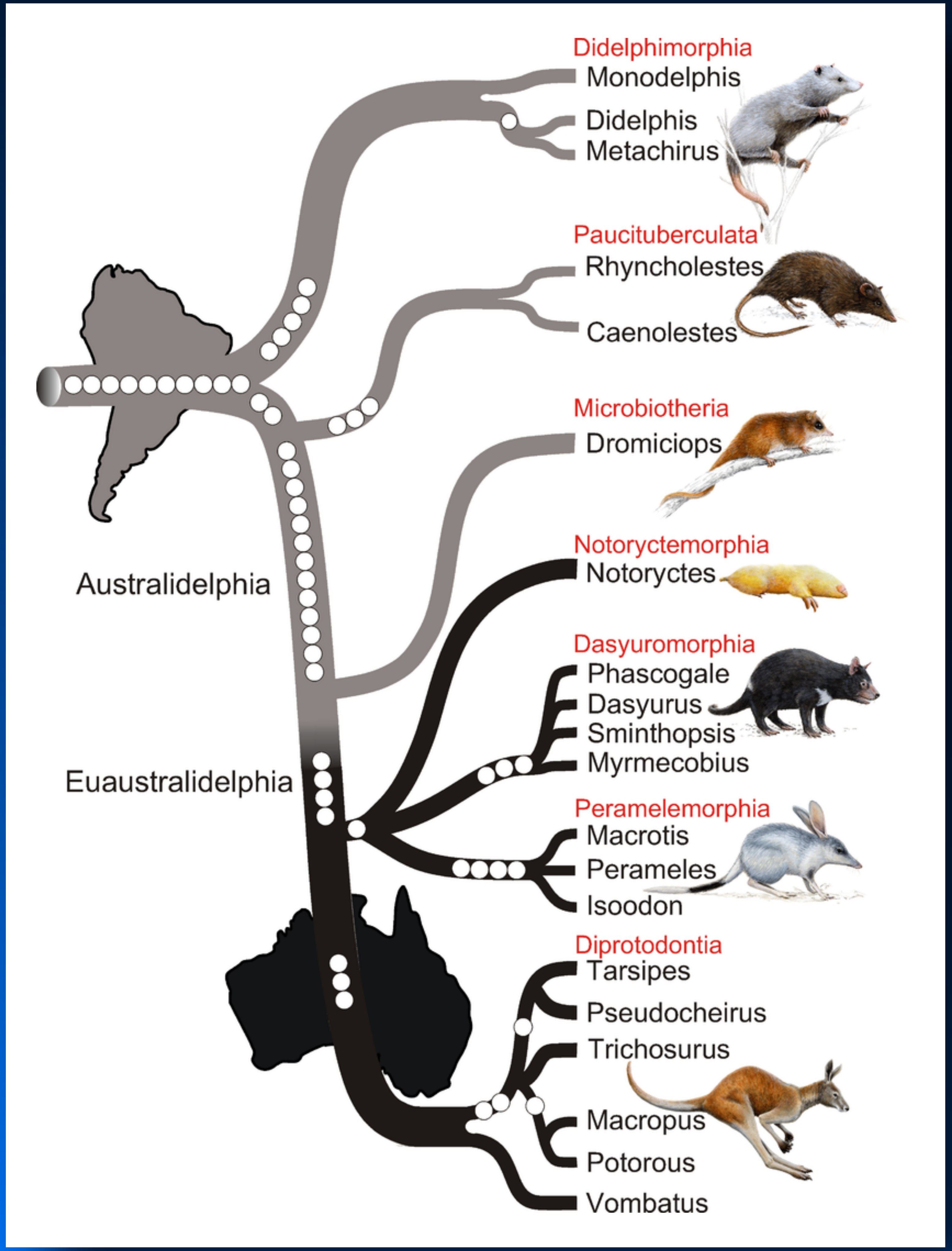
Both of these trends are consistent with the theory of evolution by natural selection and difficult to account for under other theories of evolutionary change.



Niche	Placental Mammals	Australian Marsupials
Burrower	Mole	Marsupial mole
Anteater	Lesser anteater	Numbat (anteater)
Mouse	Mouse	Marsupial mouse
Climber	Lemur	Spotted cuscus
Glider	Flying squirrel	Flying phalanger
Cat	Ocelot	Tasmanian "tiger cat"
Wolf	Wolf	Tasmanian wolf

Phylogenetics, Cladistics & Phylogeny

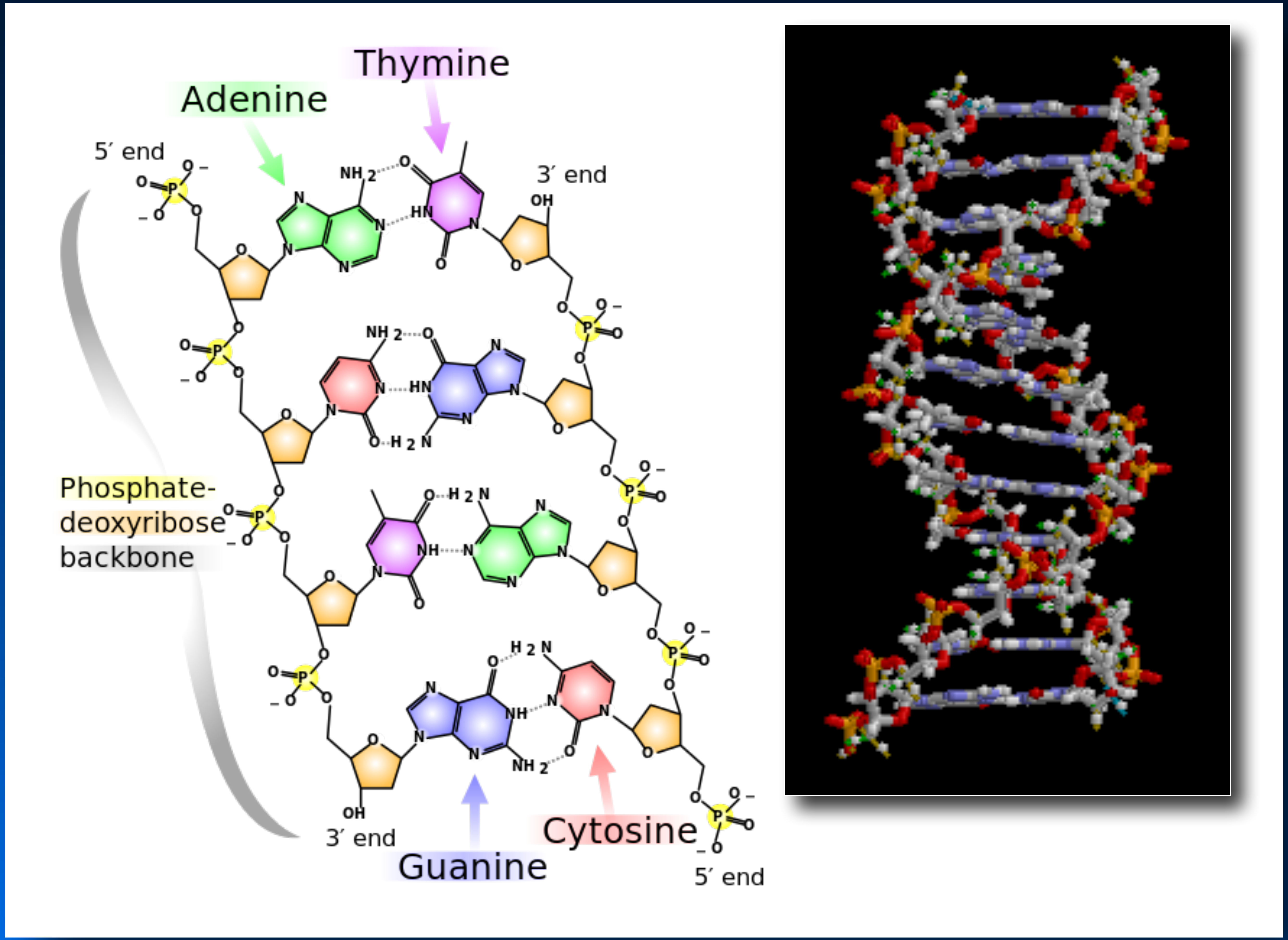
Evidence for Evolution: Biogeography



In many cases biological similar species exhibit unexpectedly disjunct geographic distributions. This can be accounted for by the groups' ancestor originating in particular geographic locations with descendant taxa owing their present distribution to historical factors (e.g., plate tectonics).

Phylogenetics, Cladistics & Phylogeny

Evidence for Evolution: Molecules



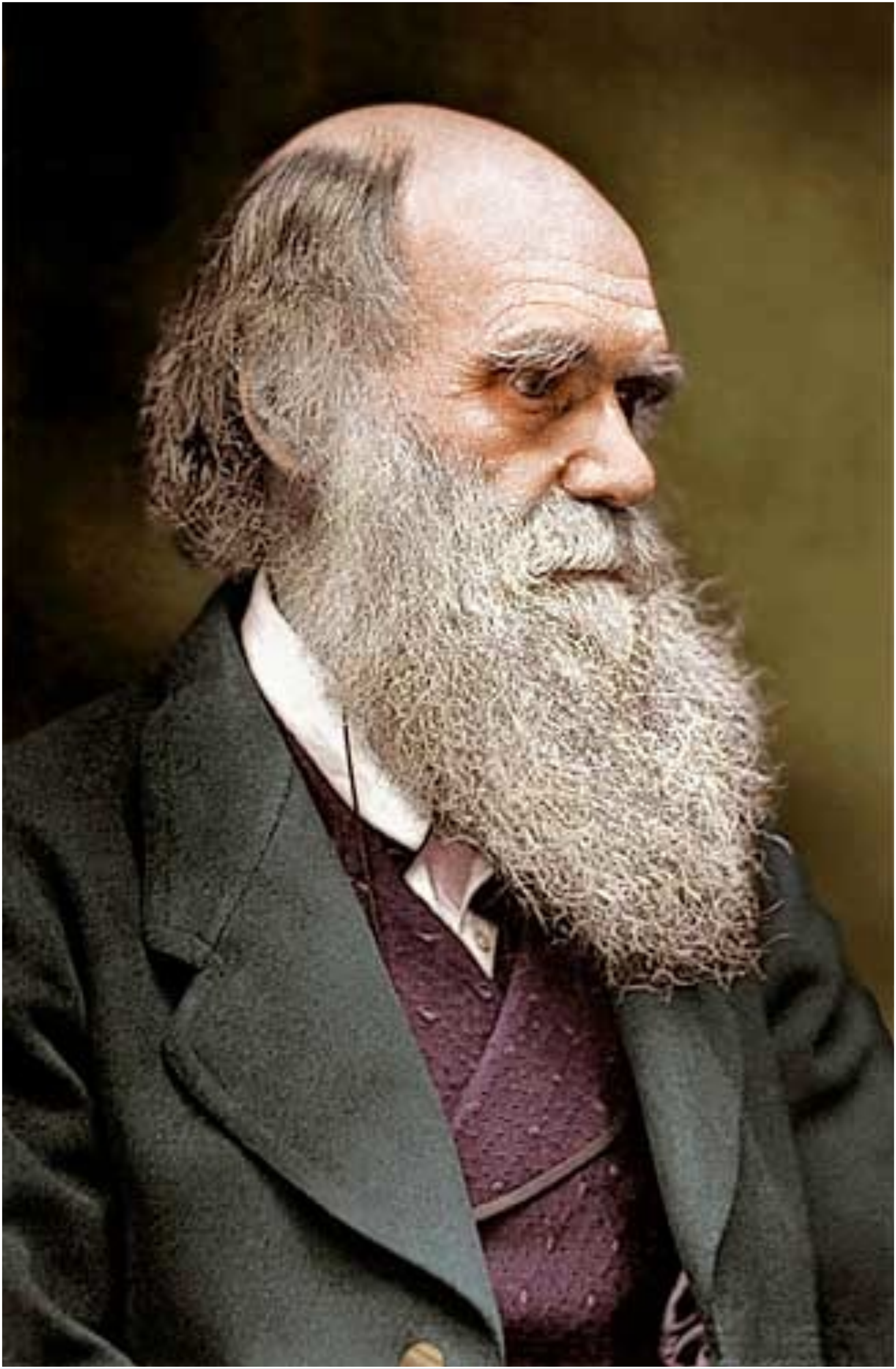
All known organisms are based on genetic information encoded either in the DNA or RNA molecule with different species differing in the sequence of the four DNA/RNA base pairs.

This is very strong evidence that all life in Earth was derived from a single ancestor without any necessity for multiple origins via spontaneous generation.

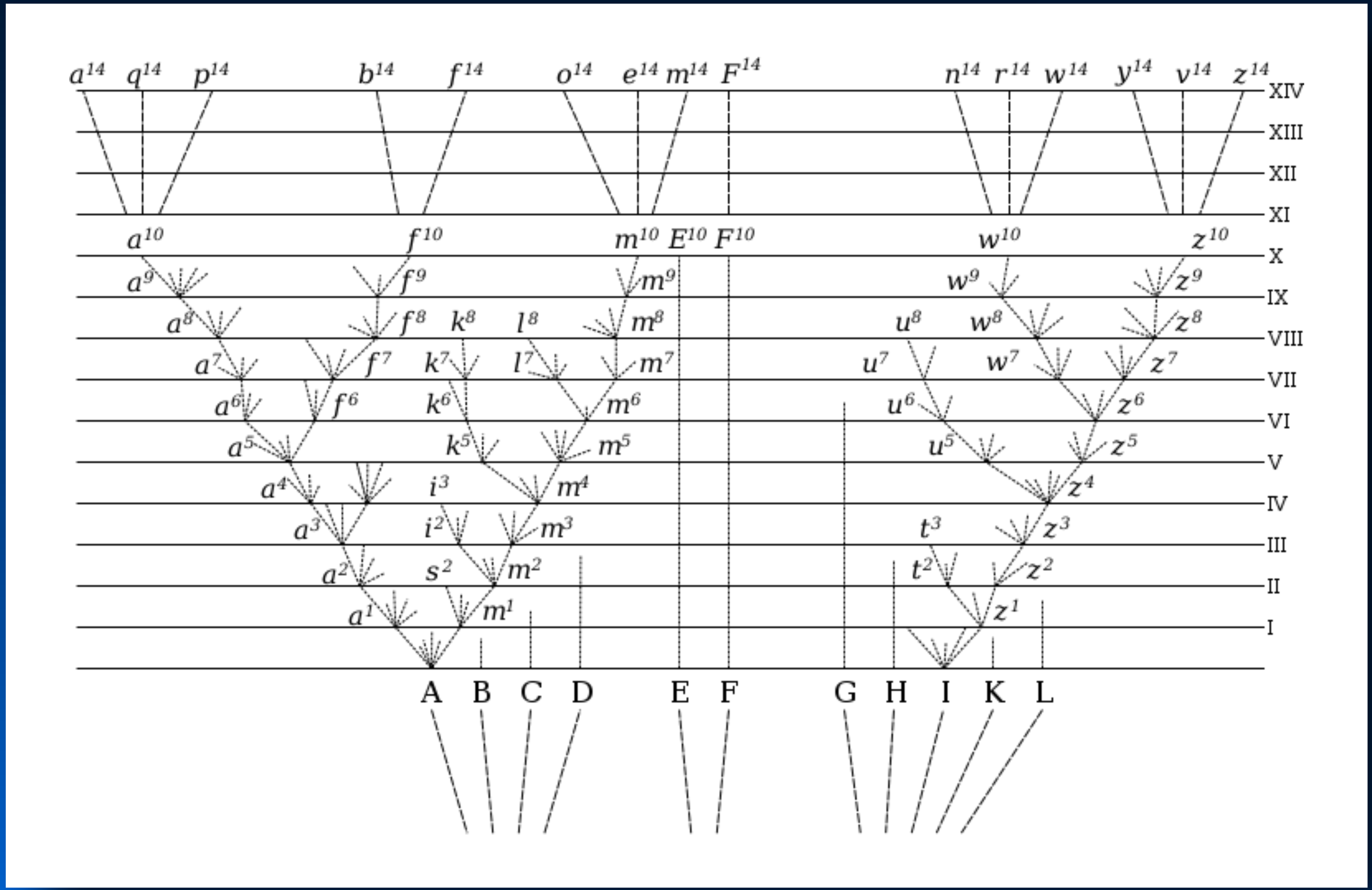
Of course, if we ever did find a living organism whose genetic code was transmitted between generations in some other way, this would imply life had many independent origins. This is a staple of much science fiction.

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent



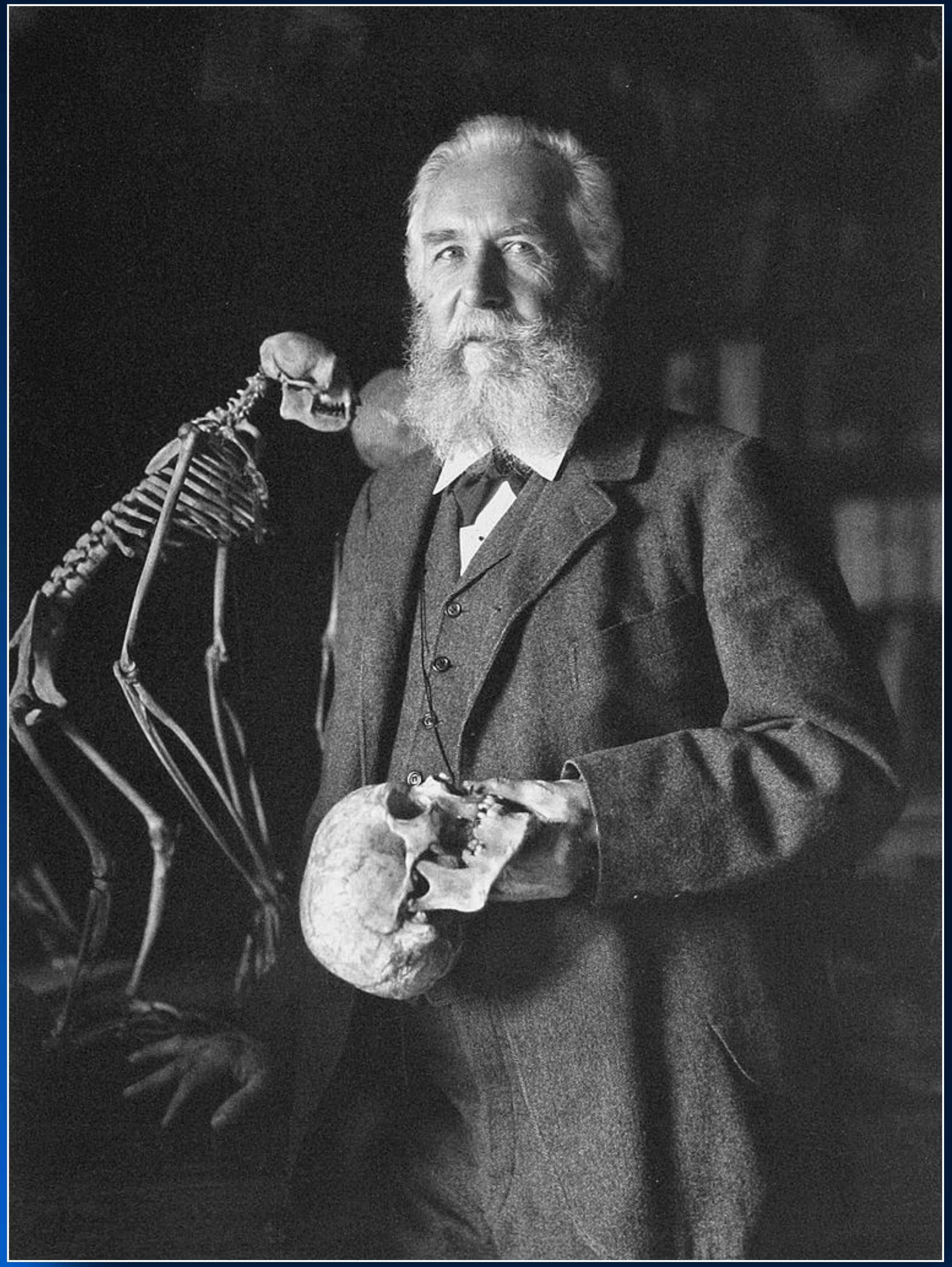
Charles Darwin
(1809 – 1882)



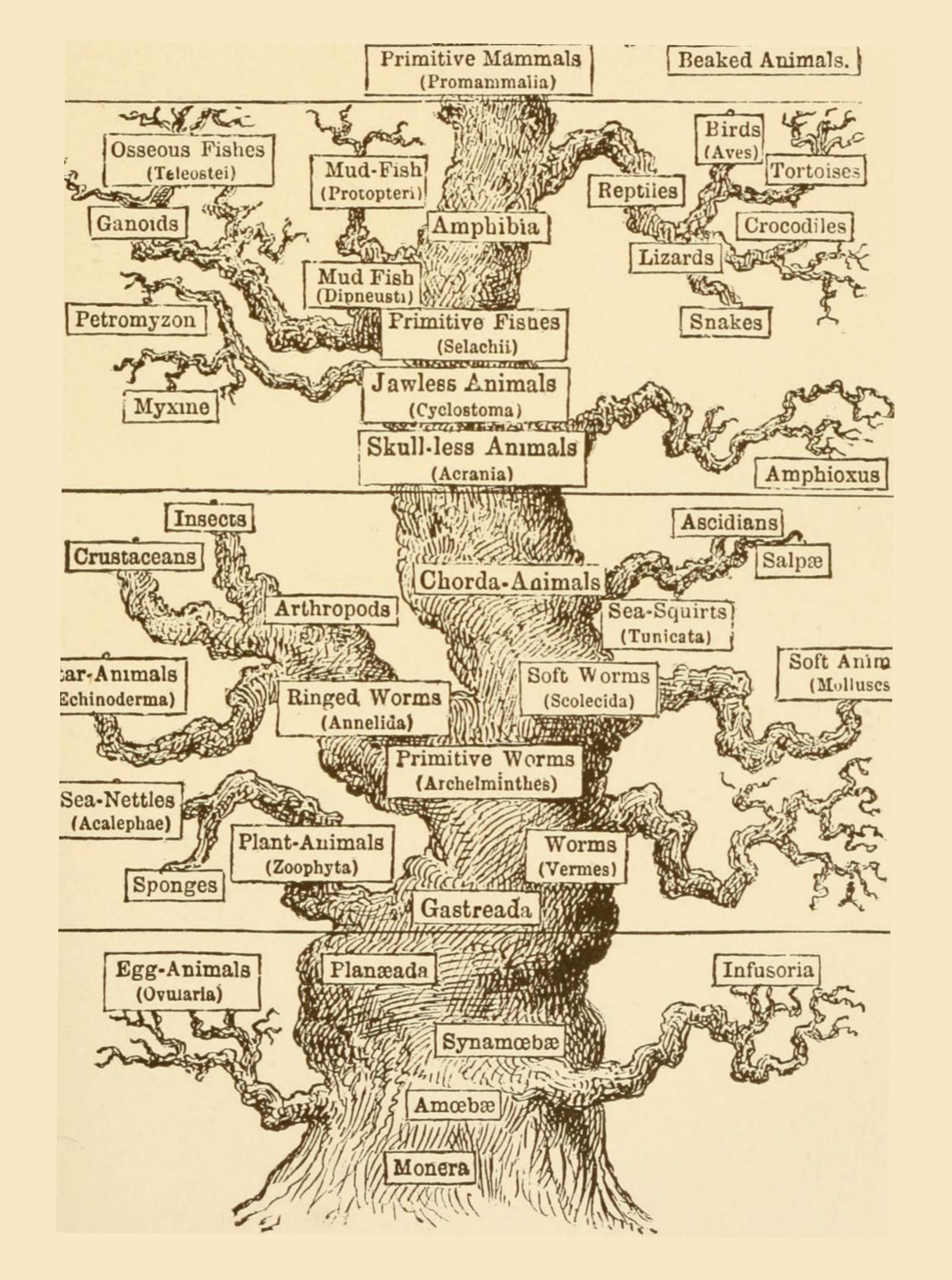
Darwin (1859)

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent



Ernst Haeckel
(1834 – 1919)



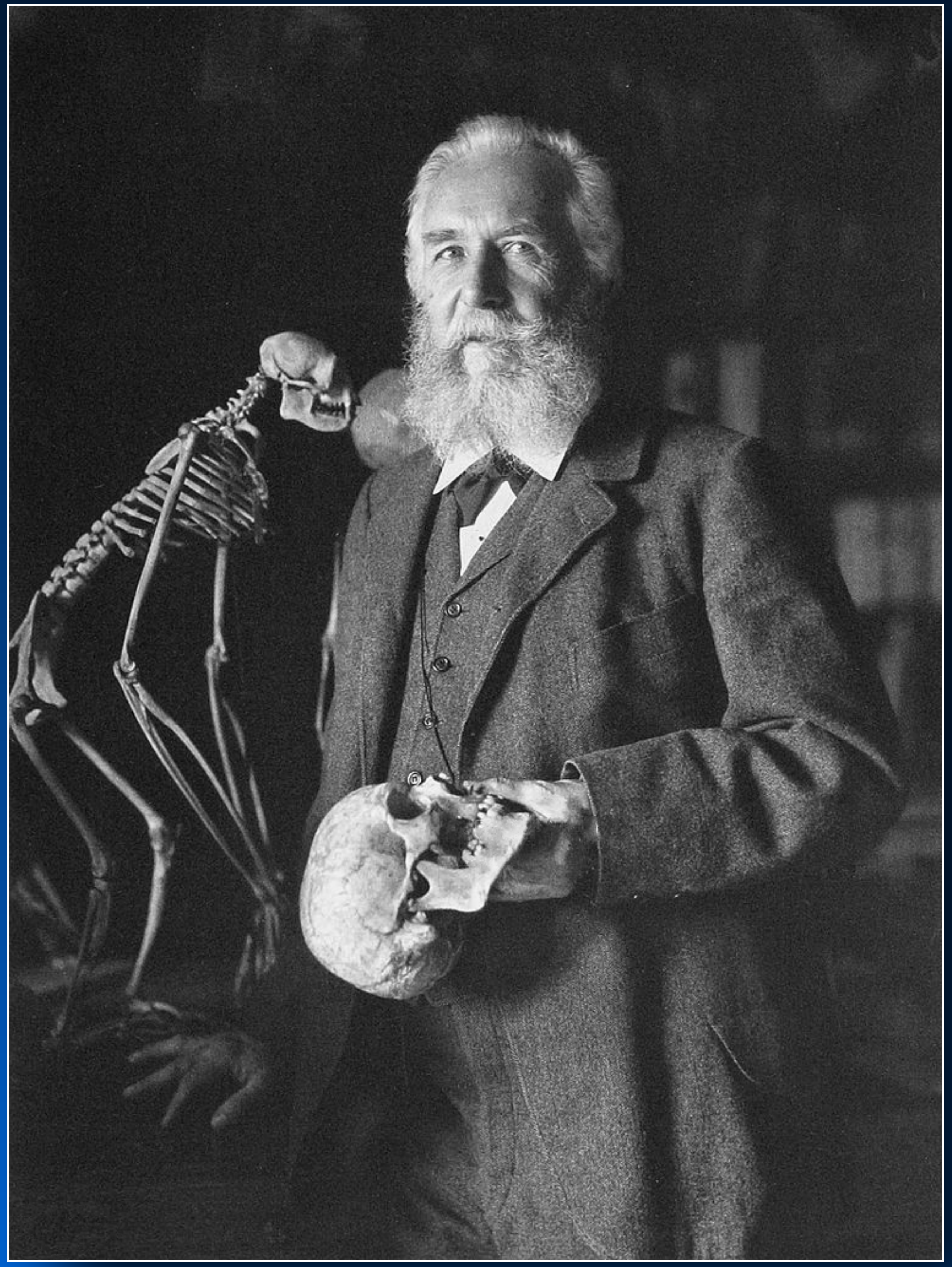
Haeckel (1874)

While Darwin (1859) did present a hypothetical geometric diagram of what he thought the hierarchical pattern of ancestry and descent might look like, the first person to attempt the inference of this pattern for living groups was Ernst Haeckel (1866).

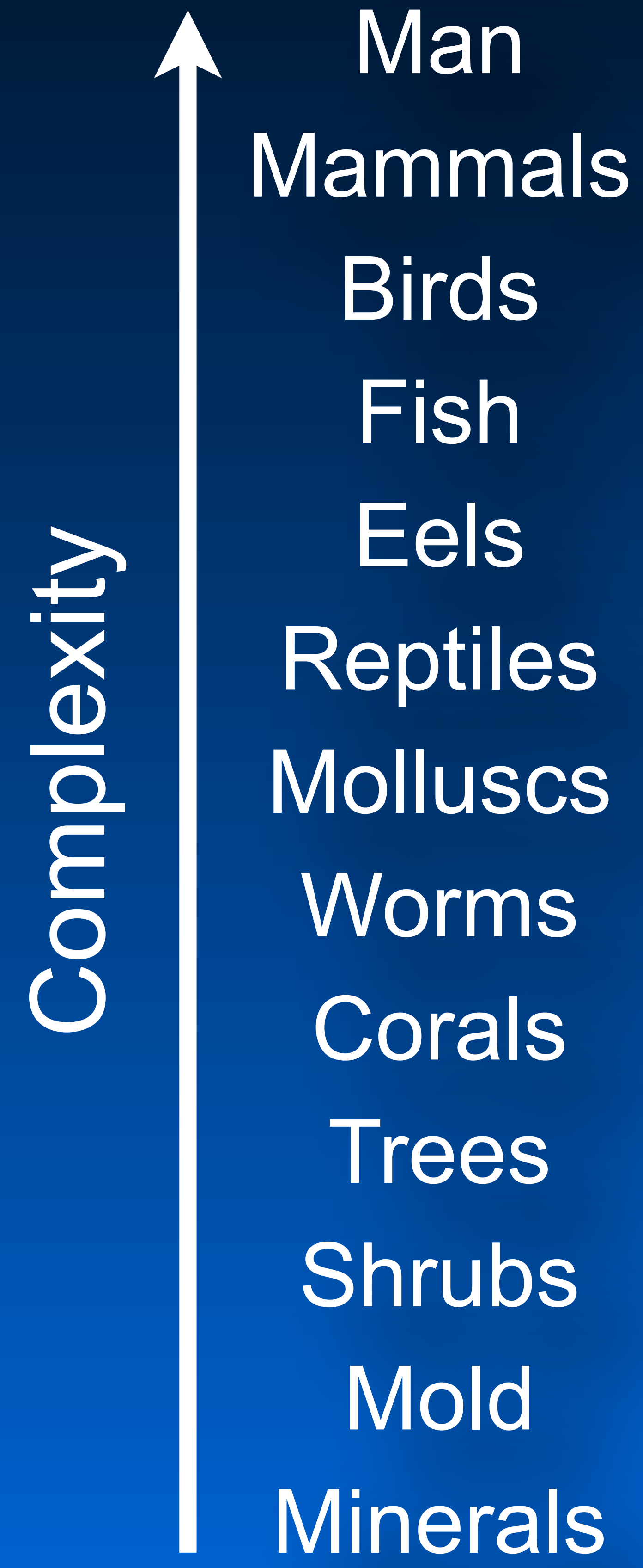
Haeckel was the first to use morphology to infer patterns of ancestry and descent, the first to use the "tree" metaphor to describe the nature of phylogenetic patterns and the first to use the technical term "phylogeny" to refer to these diagrams.

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent



Ernst Haeckel
(1834 – 1919)



Complexity

Man
Mammals
Birds
Fish
Eels
Reptiles
Molluscs
Worms
Corals
Trees
Shrubs
Mold
Minerals

Aristotelian Chain
of Being

While Darwin (1859) did present a hypothetical geometric diagram of what he thought the hierarchical pattern of ancestry and descent might look like, the first person to attempt the inference of this pattern for living groups was Ernst Haeckel (1866).

Haeckel was the first to use morphology to infer patterns of ancestry and descent, the first to use the “tree” metaphor to describe the nature of phylogenetic patterns and the first to use the technical term “phylogeny” to refer to these diagrams.

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Schools of Systematics

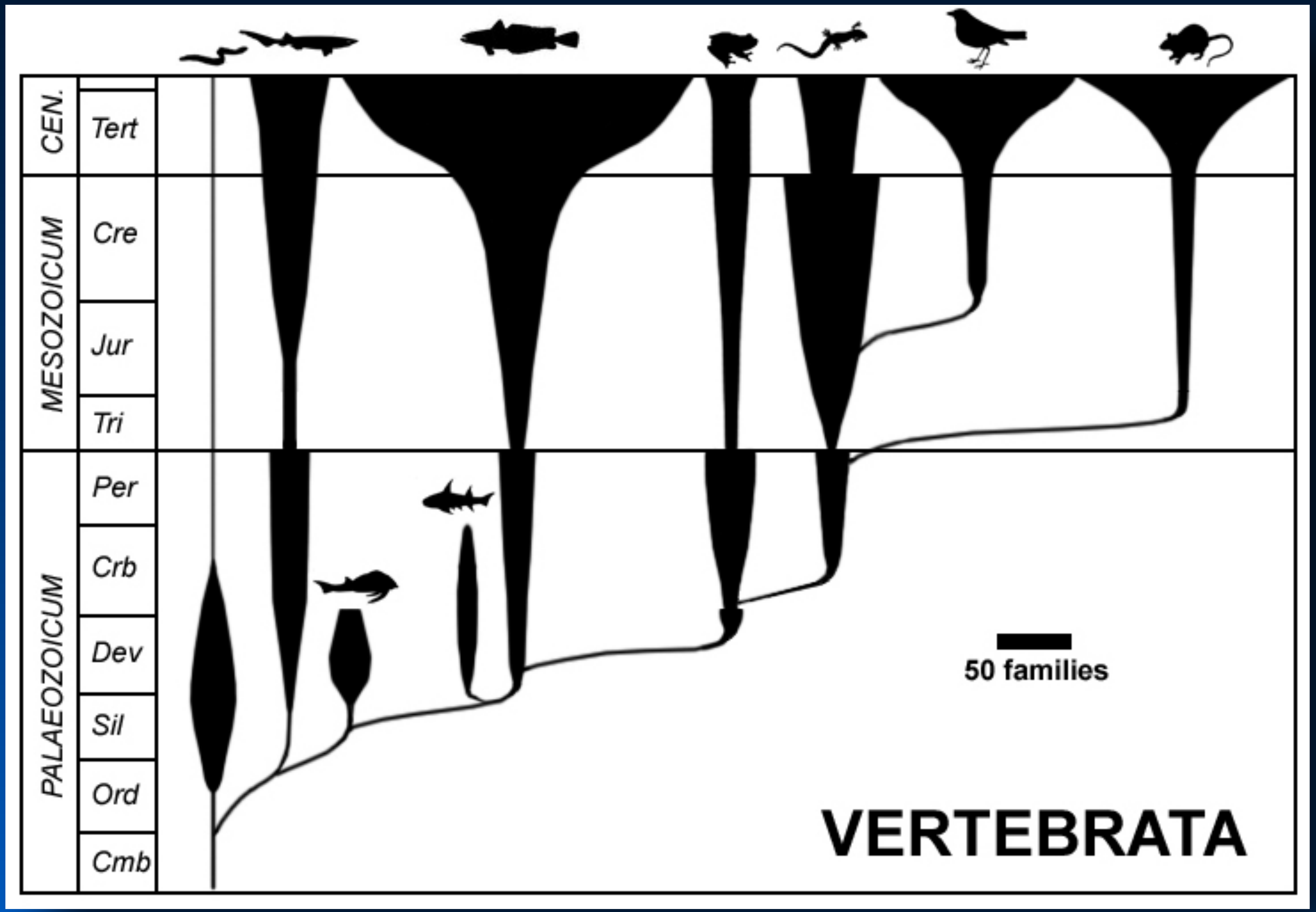
- Evolutionary Systematics - the practice of representing evolutionary relations using a combination of criteria including phylogenetic relationship, ancestor-descendant relations and degree of evolutionary change.
- Phenetic Systematics - the practice of representing evolutionary relations using an assessment of average similarities among species based on their characteristics.
  - Stratophenetics - An attempt to combine phenetic and stratigraphic evidence in the inference of phylogenetic relations.
- Phylogenetic Systematics (Cladistics) - the practice of representing evolutionary relations via the exclusive use of shared, derived characteristics (= homologies).
  - Stratocladistics - An attempt to combine cladistics and stratigraphic evidence in the inference of phylogenetic relations.

Phylogenetics, Cladistics & Phylogeny

Evolutionary Systematics

Evolutionary systematics sought to summarize and portray evolutionary relations in the form of branching diagrams, or trees.

In doing this, it included aspects of morphology, ecology, stratigraphy, geography, etc. in the definition and characterization of taxonomic entities. Thus, although birds and mammals have “reptilian” ancestors, they are distinguished as groups of equal taxonomic rank from each other and from reptiles by virtue of their (supposedly) unique and ecologically adaptive morphological characteristics (e.g., feathers, hair) and ecologies (e.g., flight, birth of live young).



This approach provides the basis for the current (Linnean) system of biological classification, but begs the question of what classifications are for.

Phylogenetics, Cladistics & Phylogeny

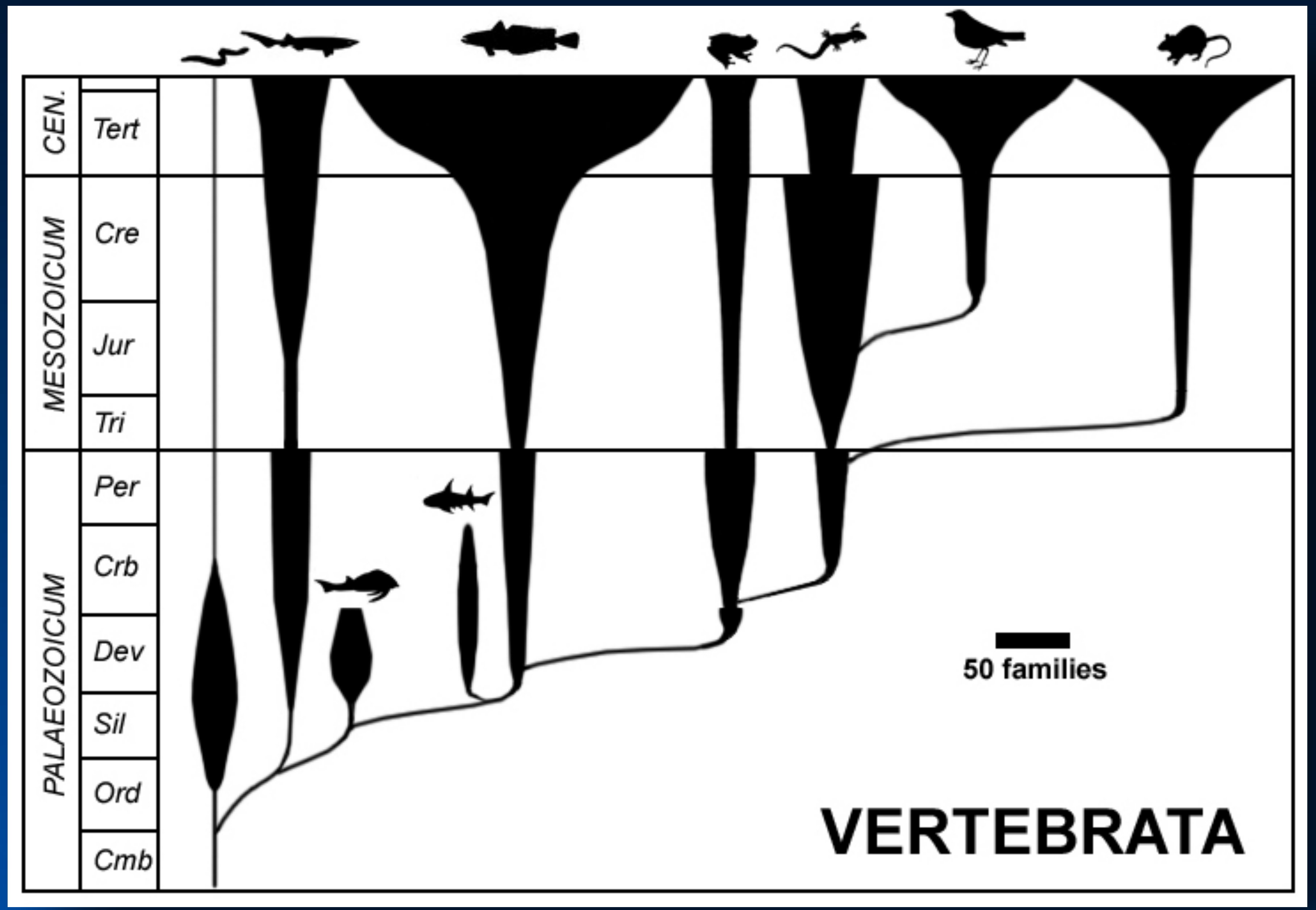
Evolutionary Systematics

Advantages

- The approach to reconstructing evolutionary relations most popular from 1859 through the 1950s.
- Seeks to create a holistic and synthetic summary of evolutionary relations by taking advantage of different sources of information.
- Employs traditional Linnean taxonomic groups.
- Based on a qualitative (narrative) approach to data analysis.
- Admits monophyletic, paraphyletic and polyphyletic groups.
- Consistent with stratigraphic record.

Disadvantages

- Inconsistent with Darwin's view of evolution.
- Subjective, with criteria being assigned different estimates of importance in different parts of the tree.
- Lacks quantitative rigor.

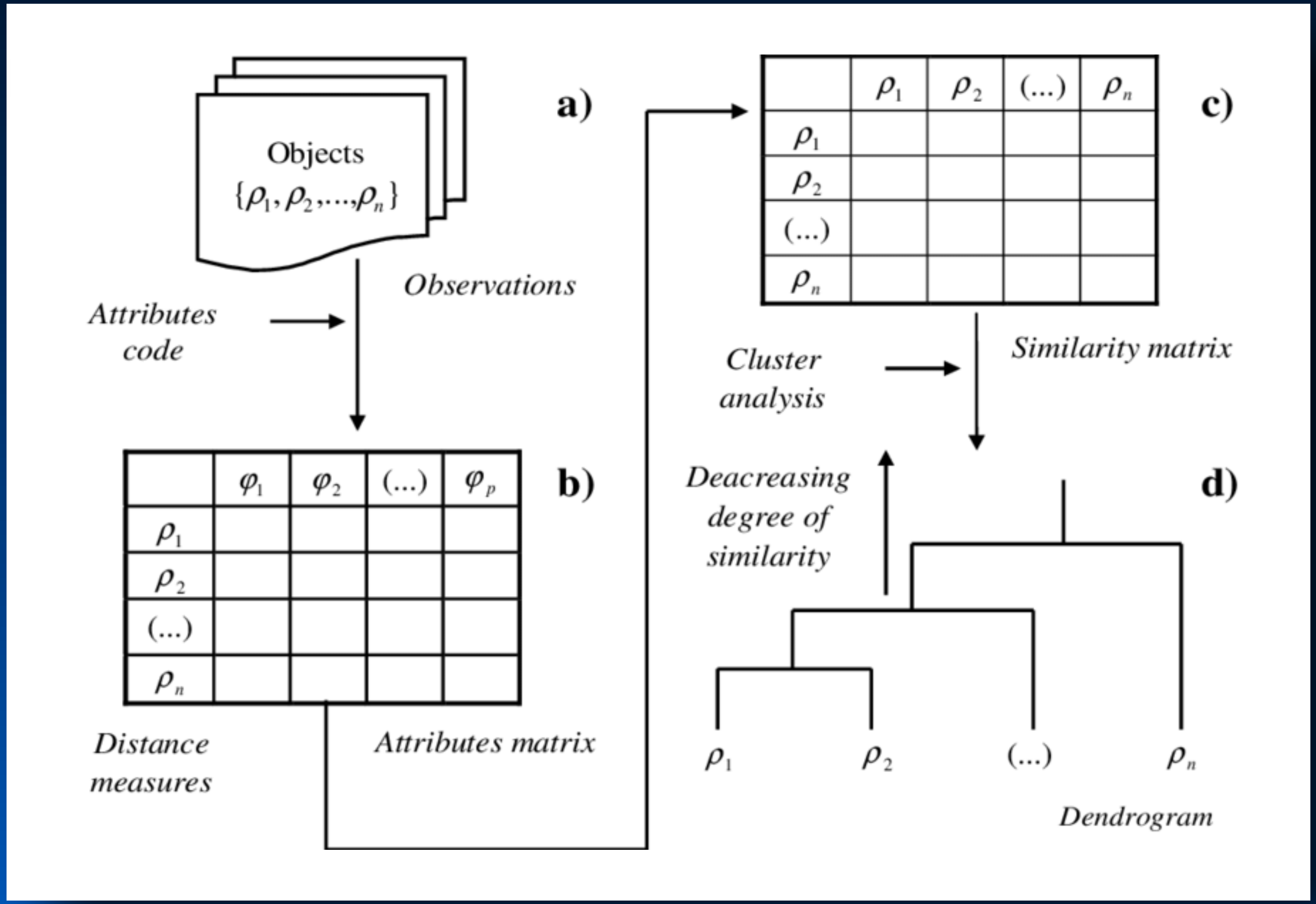


Phylogenetics, Cladistics & Phylogeny

Phenetic Systematics

Phenetic systematics sought to add objectivity and quantitative rigor to evolutionary systematics through the use of multivariate data analysis (e.g., ordination).

Taxa were described by measurements and/or numerical codes of different qualitative character states and relations between them summarized by calculating a matrix of unweighted distances that, ultimately represented patterns of average similarity, association and/or congruence. This distance matrix was then summarized graphically using multivariate procedures and both categories and classifications erected on the basis of these results.



This approach provides added objectivity and quantitative rigor to the inference of phylogenetic relations but, beyond that, was little different from evolutionary systematics.

Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy

Robert Sokal
(1926–2012)

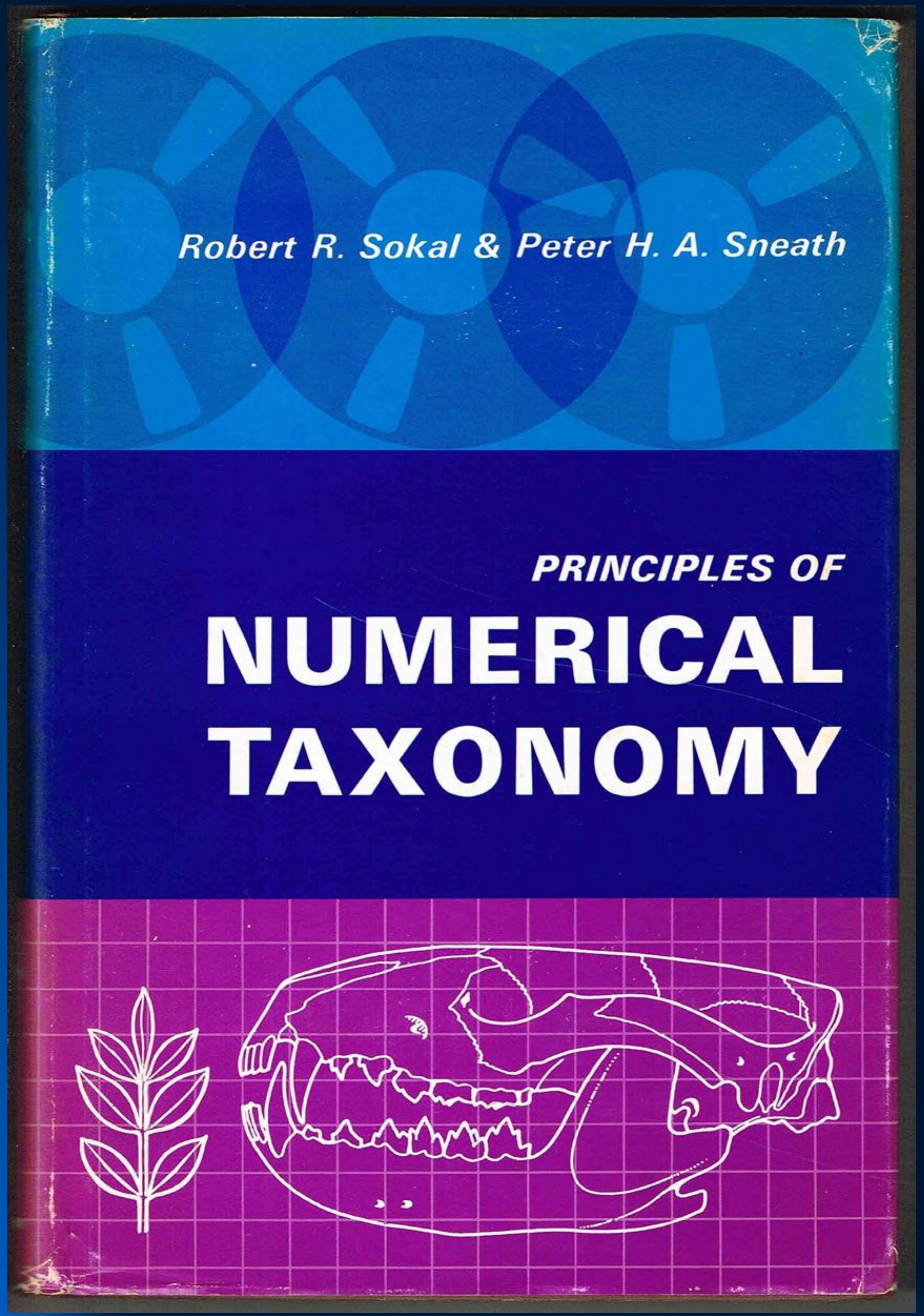
Peter H. A. Sneath
(1923–2011)

F. James Rohlf
(b. 1936)

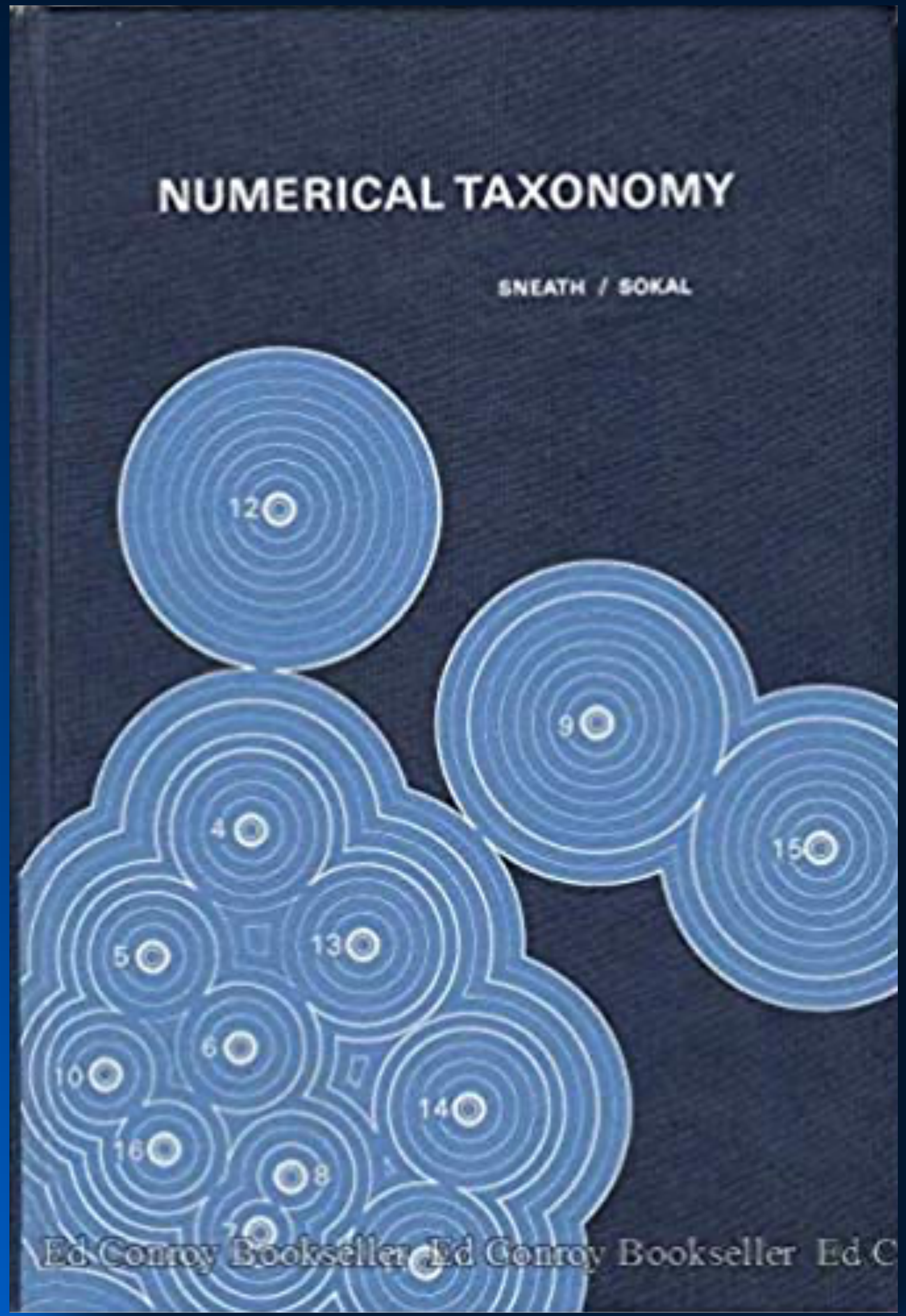
Many people contributed to the advancement of quantitative methods in systematic biology, but none more so than the numerical taxono-mists and, among that group, none more so than Robert Sokal, Peter Sneath and Jim Rohlf.

Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy



Sokal, R.R., and Sneath, P.A., 1963, Principles of numerical taxonomy: San Francisco, W. H. Freeman, 359 p.

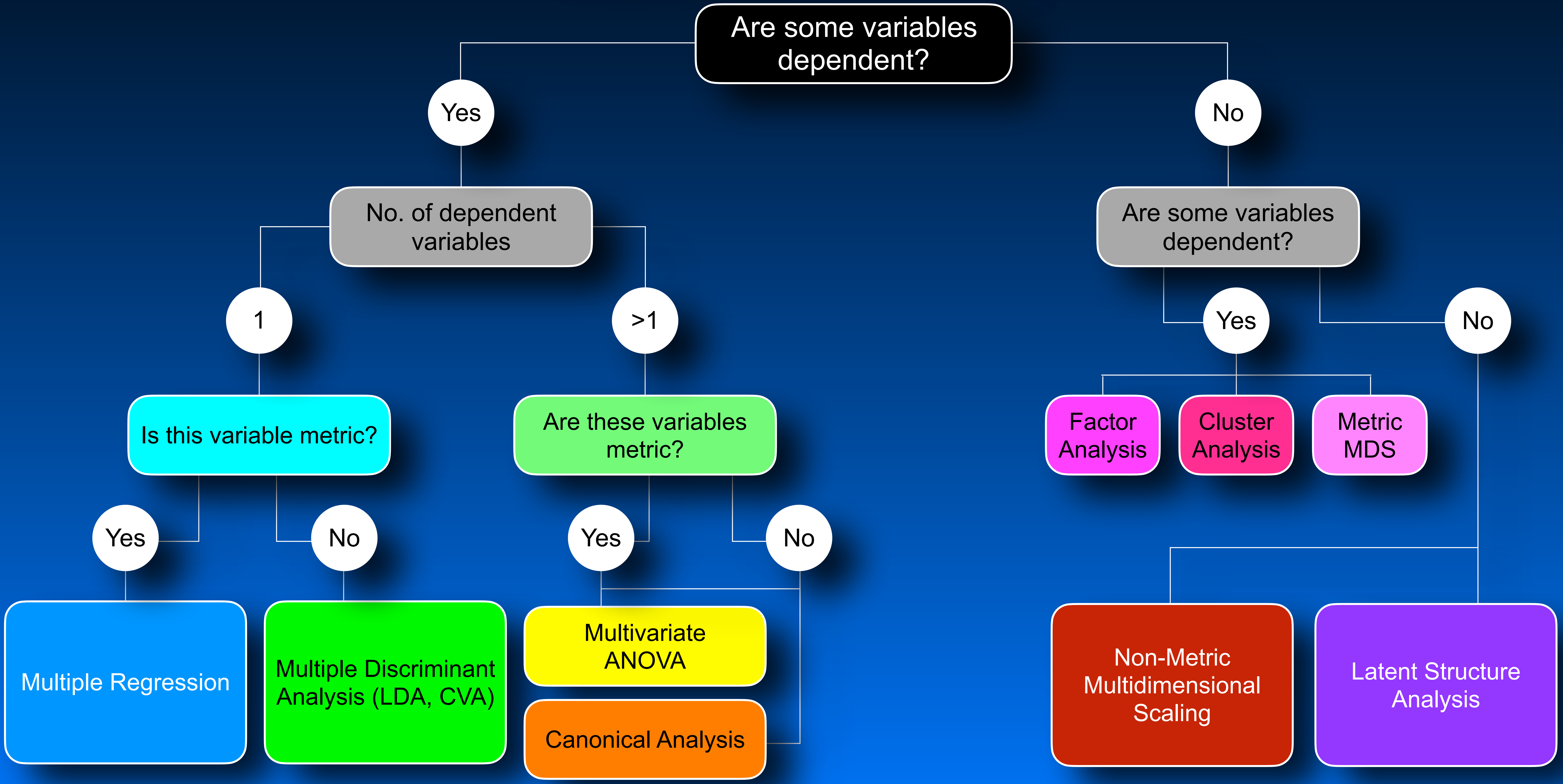


Sneath, P.H.A., and Sokal, R.R., 1973, Numerical taxonomy: the principles and practice of numerical classification: San Francisco, W. H. Freeman, 573 p.

Sokal, R.R., and Rohlf, F.J., 2012, Biometry, 4th edition: New York, W. H. Freeman and Company, 937 p.

Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy



Are some variables dependent?

Yes

No. of dependent variables

1

Is this variable metric?

Yes

Multiple Regression

No

Multiple Discriminant Analysis (LDA, CVA)

>1

Are these variables metric?

Yes

No

Multivariate ANOVA

Canonical Analysis

No

Are some variables dependent?

Yes

Factor Analysis

Cluster Analysis

Metric MDS

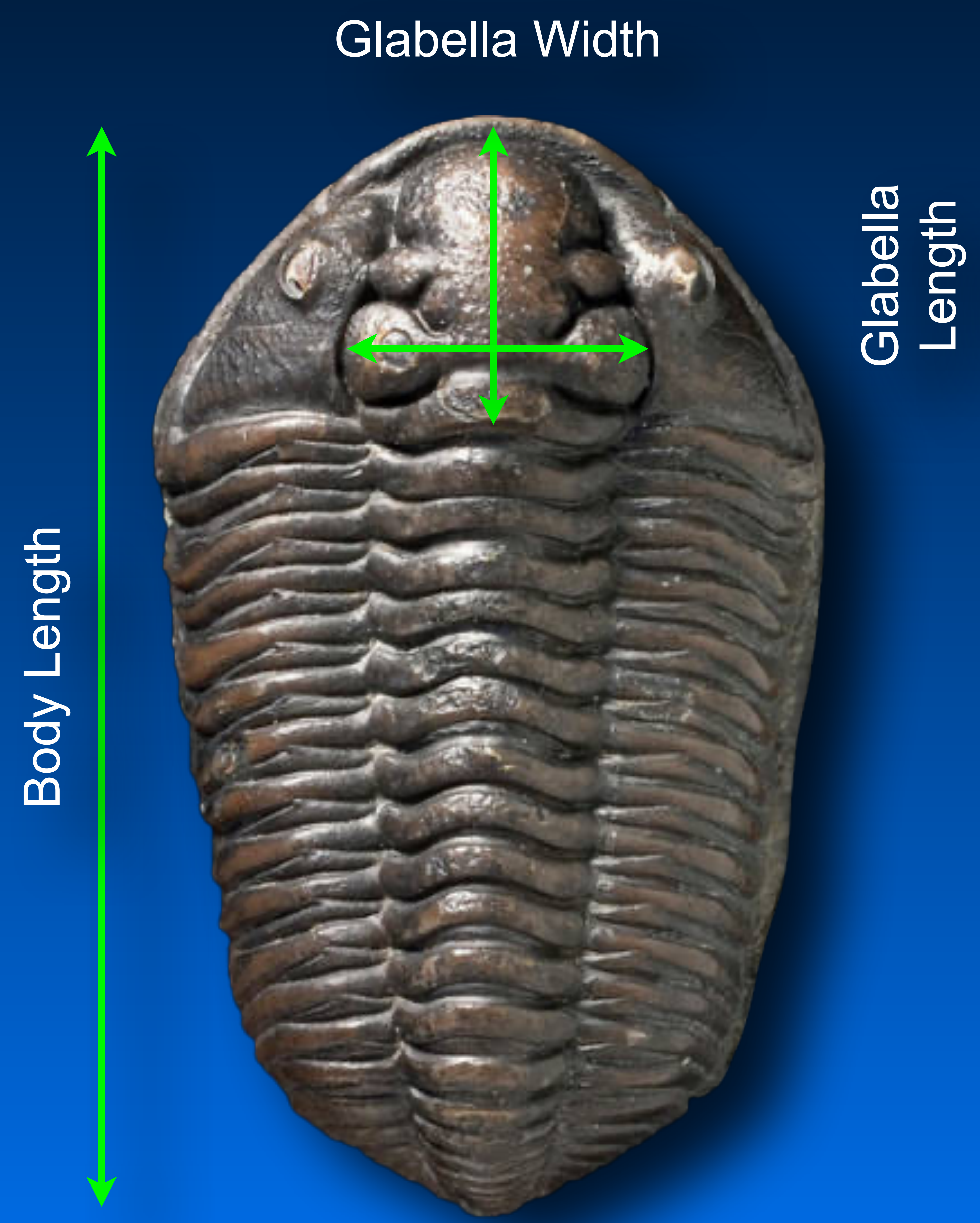
No

Non-Metric Multidimensional Scaling

Latent Structure Analysis

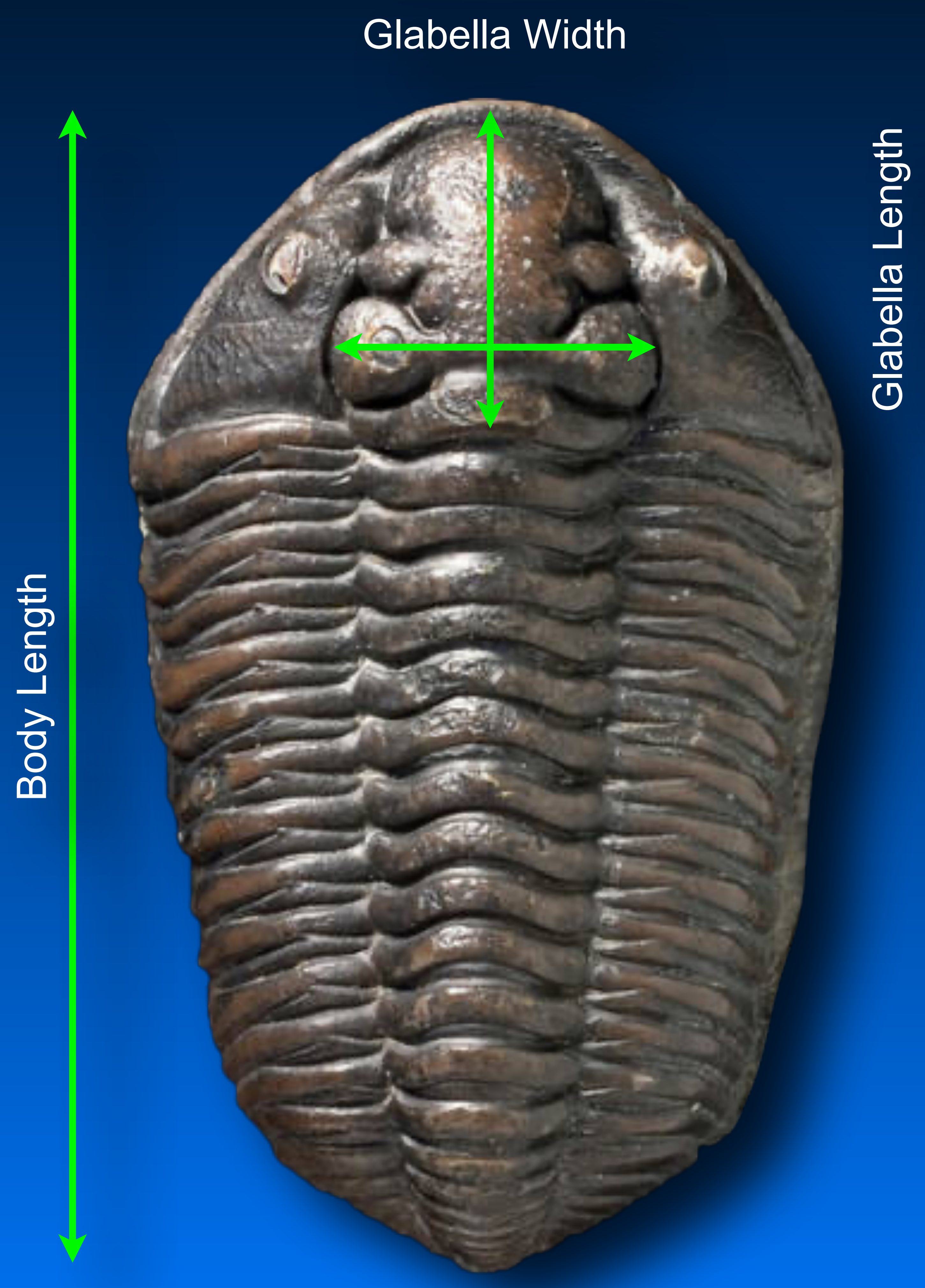
Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy: Example



Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy: Example



Genus	Body Length	Glabella Length	Glabella Width
Acaste	23.14	3.50	3.77
Balizoma	14.32	3.97	4.08
Calymene	51.69	10.91	10.72
Ceraurus	21.15	4.90	4.69
Cheirurus	31.74	9.33	12.11
Cybantyx	36.81	11.35	10.10
Cybeloides	25.13	6.39	6.81
Dalmanites	32.93	8.46	6.08
Deiphon	21.81	6.92	9.01
Ormathops	13.88	5.03	4.34
Phacopidina	21.43	7.03	6.79
Phacops	27.23	5.30	8.19
Placoparia	38.15	9.40	8.71
Pricyclopyge	40.11	14.98	12.98
Ptychoparia	62.17	12.25	8.71
Rhenops	55.94	19.00	13.10
Sphaerexoch	23.31	3.84	4.60
Toxochasmop	46.12	8.15	11.42
Trimerus	89.43	23.18	21.52
Zacanthoides	47.89	13.56	11.78

Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy: PCA

Data Matrix

Genus	Body Length	Glabella Length	Glabella Width
Acaste	23.14	3.50	3.77
Balizoma	14.32	3.97	4.08
Calymene	51.69	10.91	10.72
Ceraurus	21.15	4.90	4.69
Cheirurus	31.74	9.33	12.11
Cybantyx	36.81	11.35	10.10
Cybeloides	25.13	6.39	6.81
Dalmanites	32.93	8.46	6.08
Deiphon	21.81	6.92	9.01
Ormathops	13.88	5.03	4.34
Phacopidina	21.43	7.03	6.79
Phacops	27.23	5.30	8.19
Placoparia	38.15	9.40	8.71
Pricyclopyge	40.11	14.98	12.98
Ptychoparia	62.17	12.25	8.71
Rhenops	55.94	19.00	13.10
Sphaerexoch	23.31	3.84	4.60
Toxochasmop	46.12	8.15	11.42
Trimerus	89.43	23.18	21.52
Zacanthoides	47.89	13.56	11.78

Covariance Matrix

Component	Body Length	Glabella Length	Glabella Width
Body Length	346.892	87.191	68.416
Glabella Length	87.191	27.333	20.315
Glabella Width	68.416	20.315	18.266

Eigenvalues

Component	Eigenvalue	Variance (%)	Cum. Variance (%)
1	383.076	97.601	97.601
2	7.457	1.900	99.501
3	1.959	0.499	100.000

Eigenvectors

Component	PC-1	PC-2	PC-3
Body Length	18.606	-0.845	-0.032
Glabella Length	4.775	1.911	0.940
Glabella Width	3.755	1.758	-1.037

Eigenscores

Genus	PC-1	PC-2
Acaste	-290.93	-9.32
Balizoma	-451.63	-0.42
Calymene	301.74	-7.07
Ceraurus	-317.82	-3.34
Cheirurus	-71.77	9.21
Cybantyx	24.66	5.26
Cybeloides	-228.69	-0.13
Dalmanites	-76.42	-4.05
Deiphon	-279.67	7.55
Ormathops	-453.78	2.43
Phacopidina	-294.55	4.18
Phacops	-189.64	-1.57
Placoparia	35.06	-2.05
Pricyclopyge	114.21	14.47
Ptychoparia	495.58	-16.90
Rhenops	428.38	8.98
Sphaerexochus	-283.03	-7.35
Toxochasmops	187.56	-6.41
Trimerus	1103.07	3.46
Zacanthoides	247.67	3.07

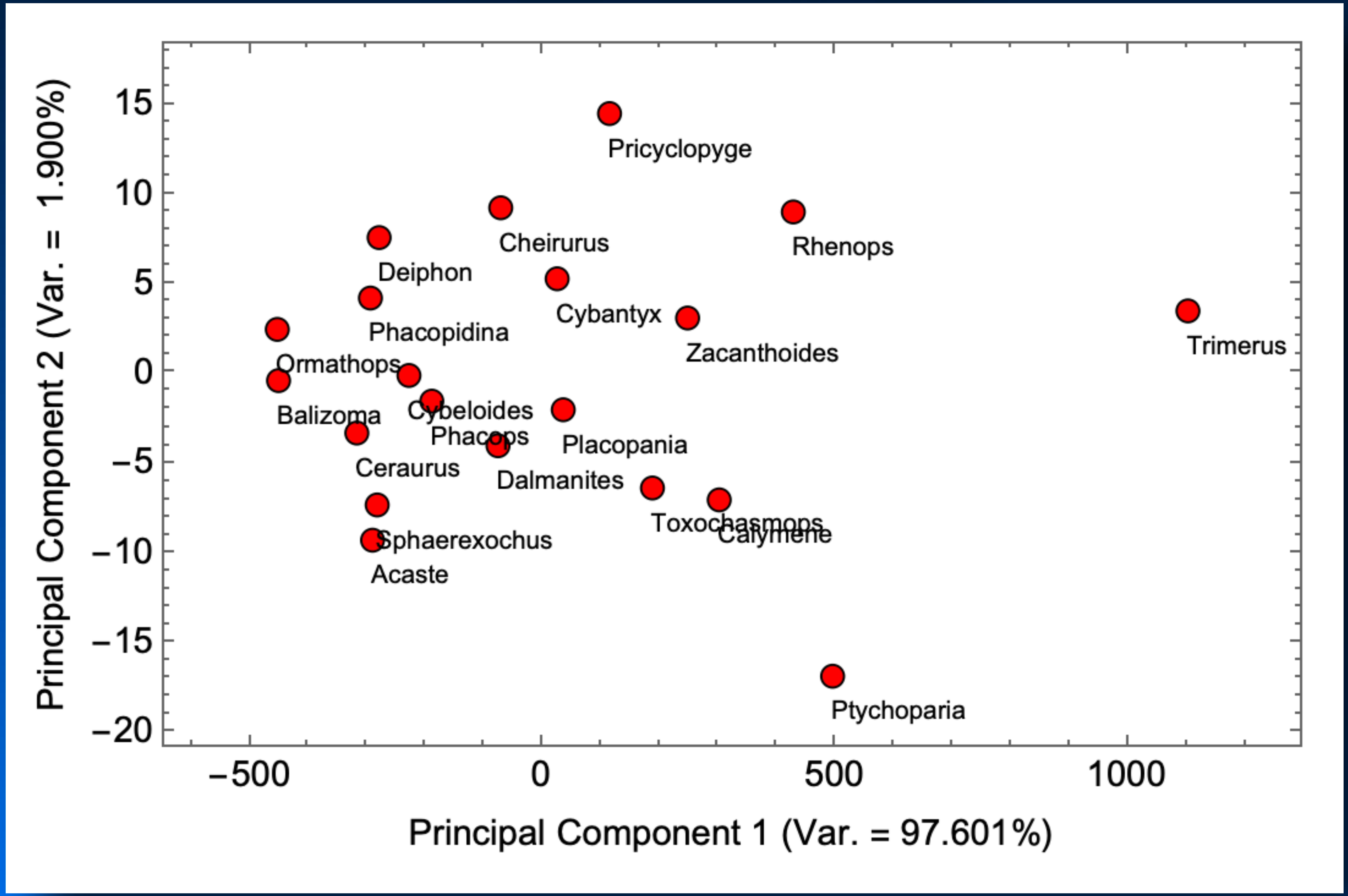
Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy: PCA

Eigenscores

Genus	PC-1	PC-2
Acaste	-290.93	-9.32
Balizoma	-451.63	-0.42
Calymene	301.74	-7.07
Ceraurus	-317.82	-3.34
Cheirurus	-71.77	9.21
Cybantyx	24.66	5.26
Cybeloides	-228.69	-0.13
Dalmanites	-76.42	-4.05
Deiphon	-279.67	7.55
Ormathops	-453.78	2.43
Phacopidina	-294.55	4.18
Phacops	-189.64	-1.57
Placoparia	35.06	-2.05
Pricyclopyge	114.21	14.47
Ptychoparia	495.58	-16.90
Rhenops	428.38	8.98
Sphaerexochus	-283.03	-7.35
Toxochasmops	187.56	-6.41
Trimerus	1103.07	3.46
Zacanthoides	247.67	3.07

Trilobite Measurements



Phylogenetics, Cladistics & Phylogeny

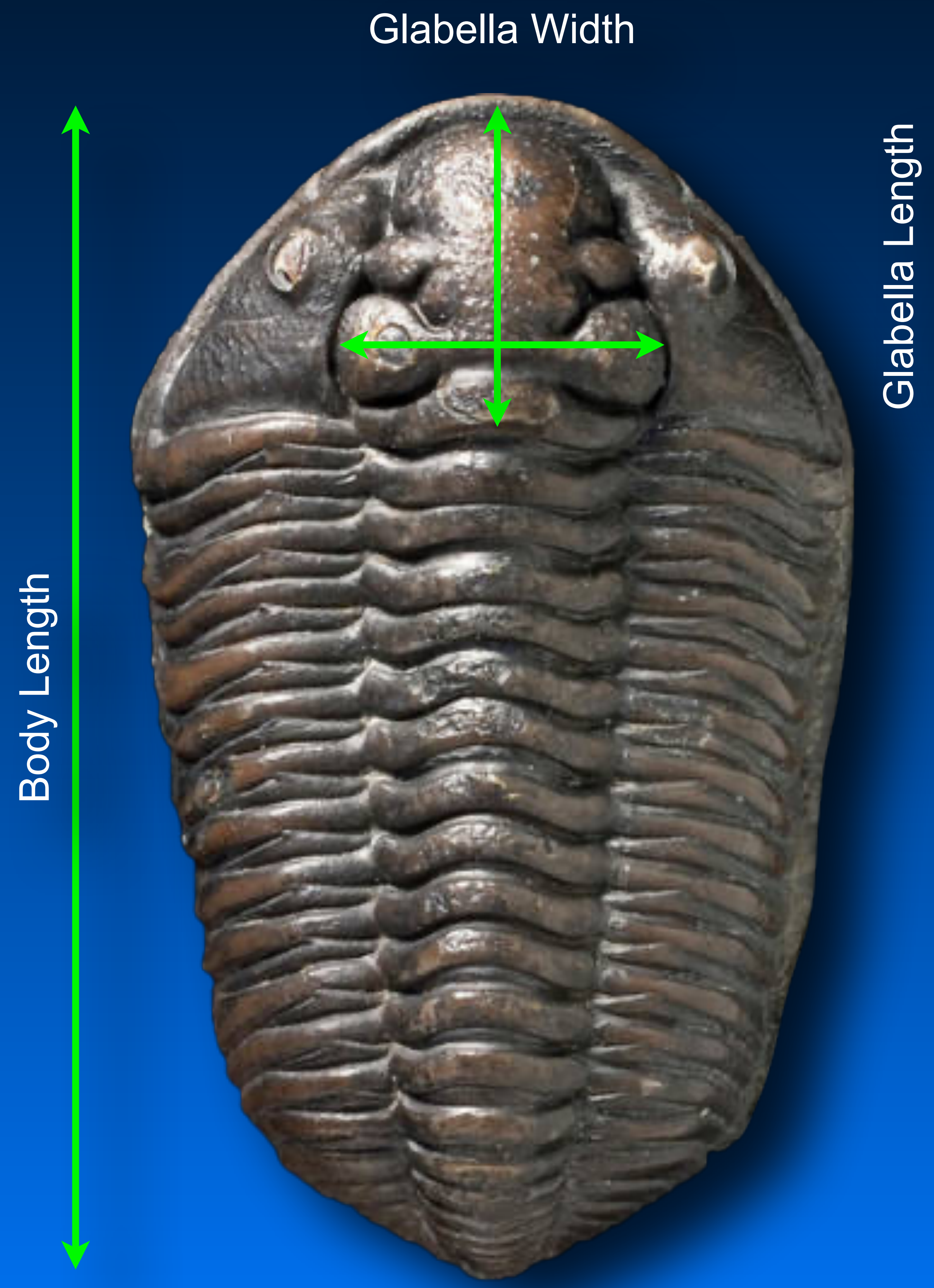
Numerical Taxonomy: Cluster Analysis

Distance Matrix

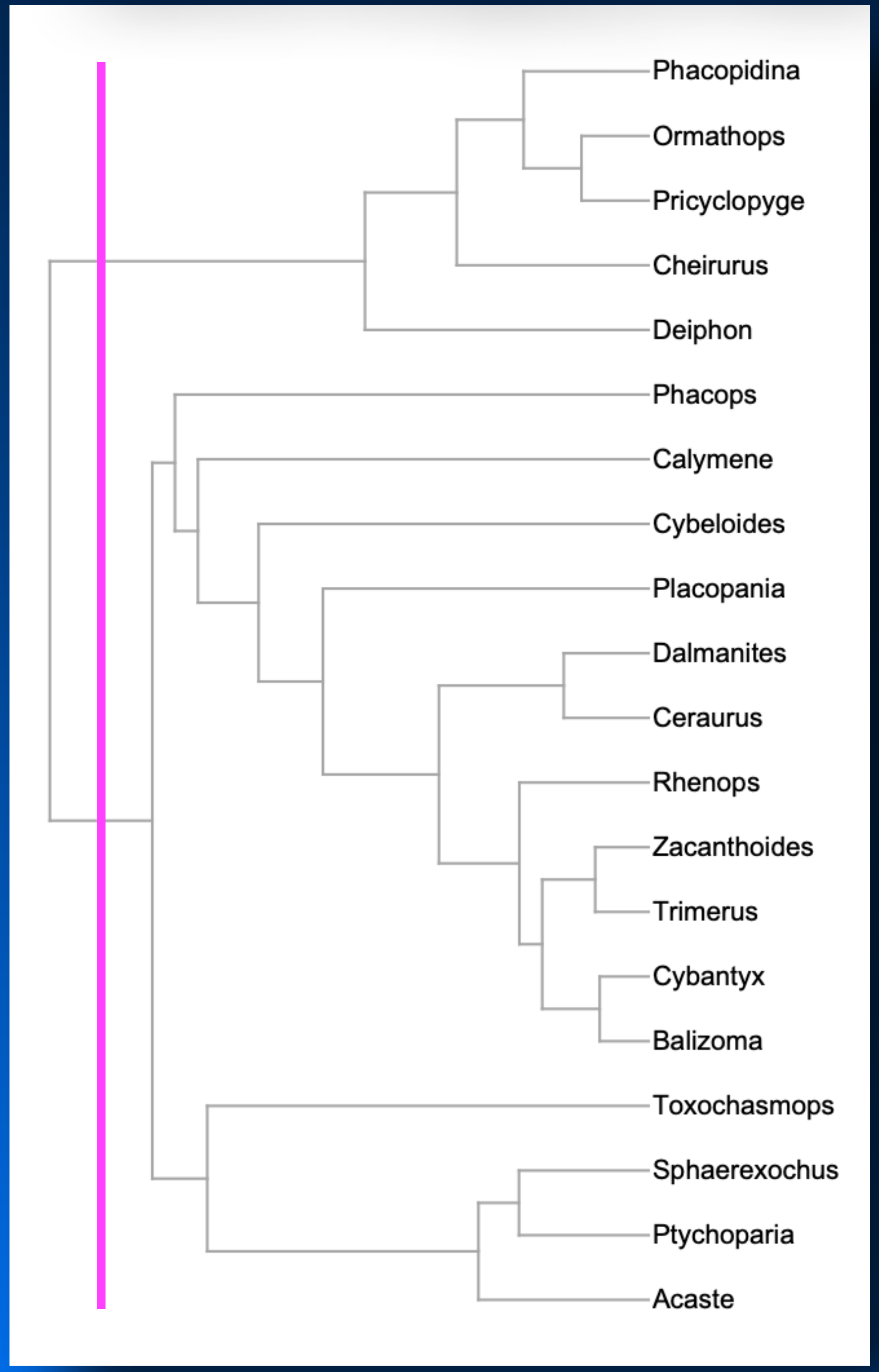
Genera	*Acaste*	*Balizoma*	*Calymene*	*Ceraurus*	*Cheirurus*	*Cybantyx*	*Cybeloides*	*Dalmanites*	*Deiphon*	*Ormathops*	*Phacopidina*	*Phacops*	*Placoparia*	*Pricyclopyge*	*Ptychoparia*	*Rhenops*	*Sphaerexochus*	*Sphaerexochus*	*Trimerus*	*Zacanthoides*
Acaste	0.00	8.84	30.30	2.60	13.32	16.99	4.64	11.22	6.40	9.40	4.95	6.29	16.87	22.46	40.30	37.46	0.91	24.66	71.39	27.89
Balizoma	8.84	0.00	38.58	6.92	19.92	24.42	11.41	19.25	9.44	1.18	8.20	13.61	24.88	29.42	48.78	45.16	9.01	32.90	79.47	35.75
Calymene	30.30	38.58	0.00	31.70	20.06	14.90	27.22	19.48	30.19	38.79	30.76	25.22	13.77	12.48	10.75	9.44	29.88	6.26	41.13	4.75
Ceraurus	2.60	6.92	31.70	0.00	13.67	17.78	4.75	12.38	4.81	7.28	3.00	7.03	18.04	23.02	41.87	38.47	2.41	26.06	72.66	28.99
Cheirurus	13.32	19.92	20.06	13.67	0.00	5.82	8.97	6.21	10.68	19.95	11.83	7.21	7.26	10.14	30.76	26.08	12.55	14.44	60.07	16.70
Cybantyx	16.99	24.42	14.90	17.78	5.82	0.00	13.11	6.29	15.68	24.47	16.31	11.49	2.74	5.69	25.41	20.82	16.40	9.93	55.13	11.42
Cybeloides	4.64	11.41	27.22	4.75	8.97	13.11	0.00	8.10	4.02	11.60	3.75	2.74	13.50	18.34	37.55	33.88	3.83	21.56	68.06	24.37
Dalmanites	11.22	19.25	19.48	12.38	6.21	6.29	8.10	0.00	11.60	19.43	11.61	6.85	5.92	11.90	29.60	26.26	10.77	14.23	60.39	16.80
Deiphon	6.40	9.44	30.19	4.81	10.68	15.68	4.02	11.60	0.00	9.39	2.25	5.72	16.53	20.39	40.71	36.44	5.58	24.46	70.66	27.05
Ormathops	9.40	1.18	38.79	7.28	19.95	24.47	11.60	19.43	9.39	0.00	8.19	13.90	25.04	29.35	49.02	45.18	9.51	33.16	79.58	35.84
Phacopidina	4.95	8.20	30.76	3.00	11.83	16.31	3.75	11.61	2.25	8.19	0.00	6.21	17.00	21.22	41.12	37.07	4.30	25.15	71.43	27.71
Phacops	6.29	13.61	25.22	7.03	7.21	11.49	2.74	6.85	5.72	13.90	6.21	0.00	11.68	16.81	35.63	32.19	5.51	19.37	66.08	22.54
Placoparia	16.87	24.88	13.77	18.04	7.26	2.74	13.50	5.92	16.53	25.04	17.00	11.68	0.00	7.29	24.19	20.69	16.37	8.51	54.62	11.03
Pricyclopyge	22.46	29.42	12.48	23.02	10.14	5.69	18.34	11.90	20.39	29.35	21.22	16.81	7.29	0.00	22.63	16.33	21.83	9.23	50.72	8.00
Ptychoparia	40.30	48.78	10.75	41.87	30.76	25.41	37.55	29.60	40.71	49.02	41.12	35.63	24.19	22.63	0.00	10.18	39.97	16.79	32.04	14.66
Rhenops	37.46	45.16	9.44	38.47	26.08	20.82	33.88	26.26	36.44	45.18	37.07	32.19	20.69	16.33	10.18	0.00	36.97	14.73	34.78	9.81
Sphaerexochus	0.91	9.01	29.88	2.41	12.55	16.40	3.83	10.77	5.58	9.51	4.30	5.51	16.37	21.83	39.97	36.97	0.00	24.19	70.94	27.39
Toxochasmops	24.66	32.90	6.26	26.06	14.44	9.93	21.56	14.23	24.46	33.16	25.15	19.37	8.51	9.23	16.79	14.73	24.19	0.00	46.94	5.70
Trimerus	71.39	79.47	41.13	72.66	60.07	55.13	68.06	60.39	70.66	79.58	71.43	66.08	54.62	50.72	32.04	34.78	70.94	46.94	0.00	43.74
Zacanthoides	27.89	35.75	4.75	28.99	16.70	11.42	24.37	16.80	27.05	35.84	27.71	22.54	11.03	8.00	14.66	9.81	27.39	5.70	43.74	0.00

Phylogenetics, Cladistics & Phylogeny

Numerical Taxonomy: Cluster Analysis



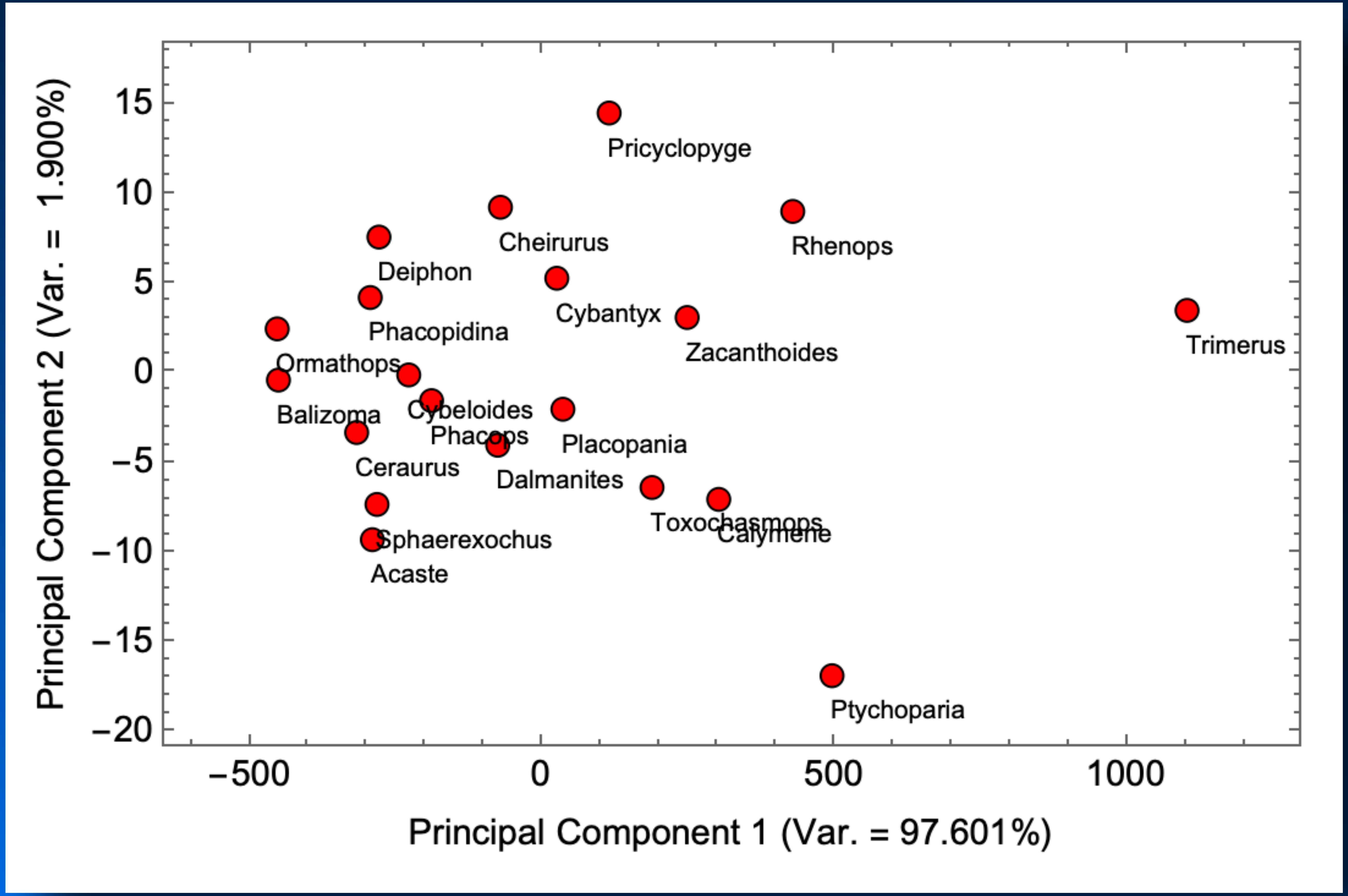
Unweighted Pair Group Method Averaging (UPGMA)



Phylogenetics, Cladistics & Phylogeny

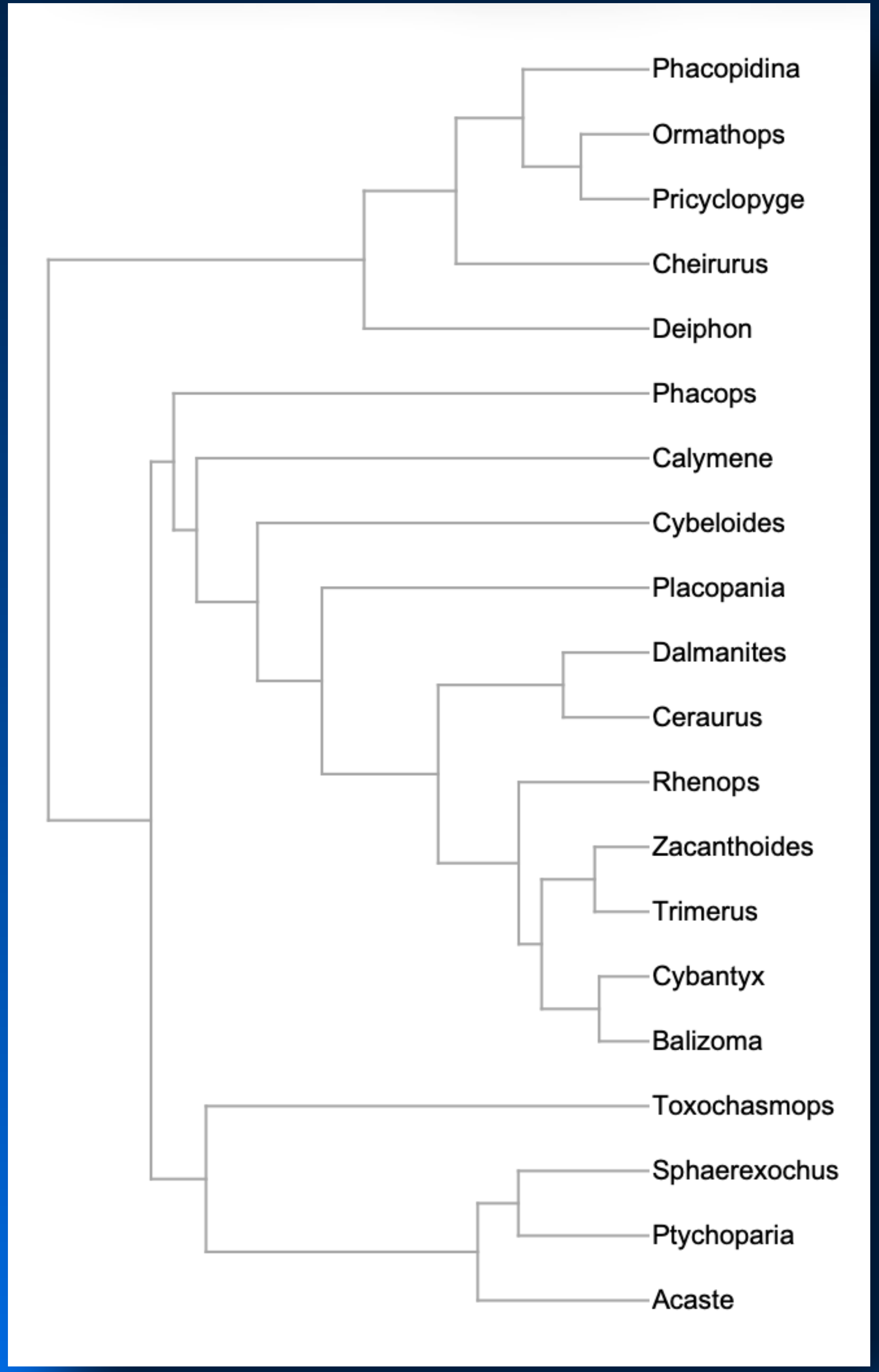
Numerical Taxonomy

Principal Component Analysis (Covariance Matrix)



Which result is correct?

Unweighted Pair Group Method Averaging (UPGMA)



They both are! 🤪

Phylogenetics, Cladistics & Phylogeny

Stratophenetics

Stratophenetics represents an attempt to include patterns of stratigraphic first appearances as criteria that could be used to infer phylogenetic relations in an overall phenetic context.

Species recognized operationally as "phenetic clusters of very similar individuals." (p. 48).

"The approach requires a relatively dense and continuous fossil record. Where this record is available, a stratophenetic approach gives the most direct and complete reading of phylogeny possible." (p. 50)

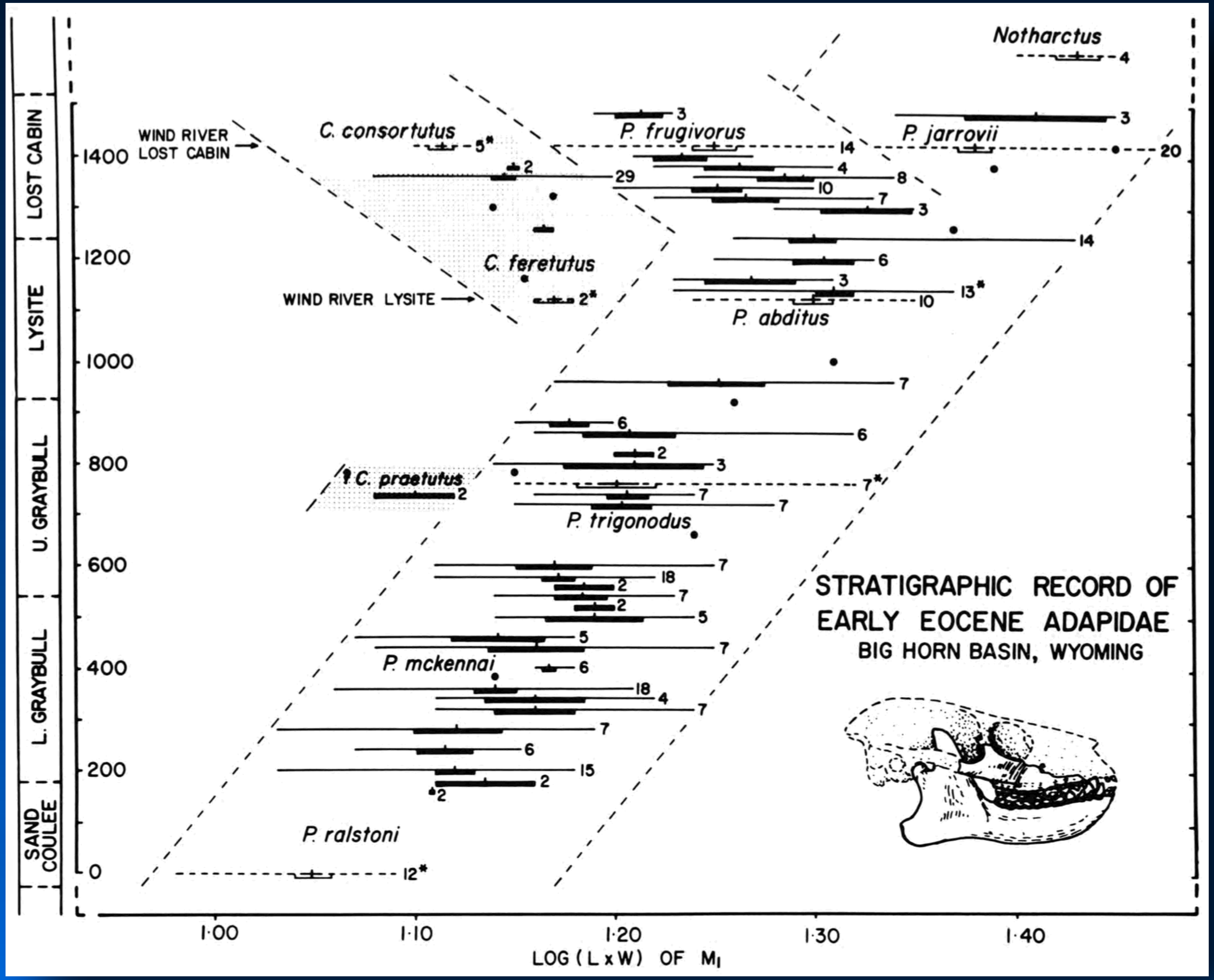


Diagram from Gingerich (1979)

Phylogenetics, Cladistics & Phylogeny

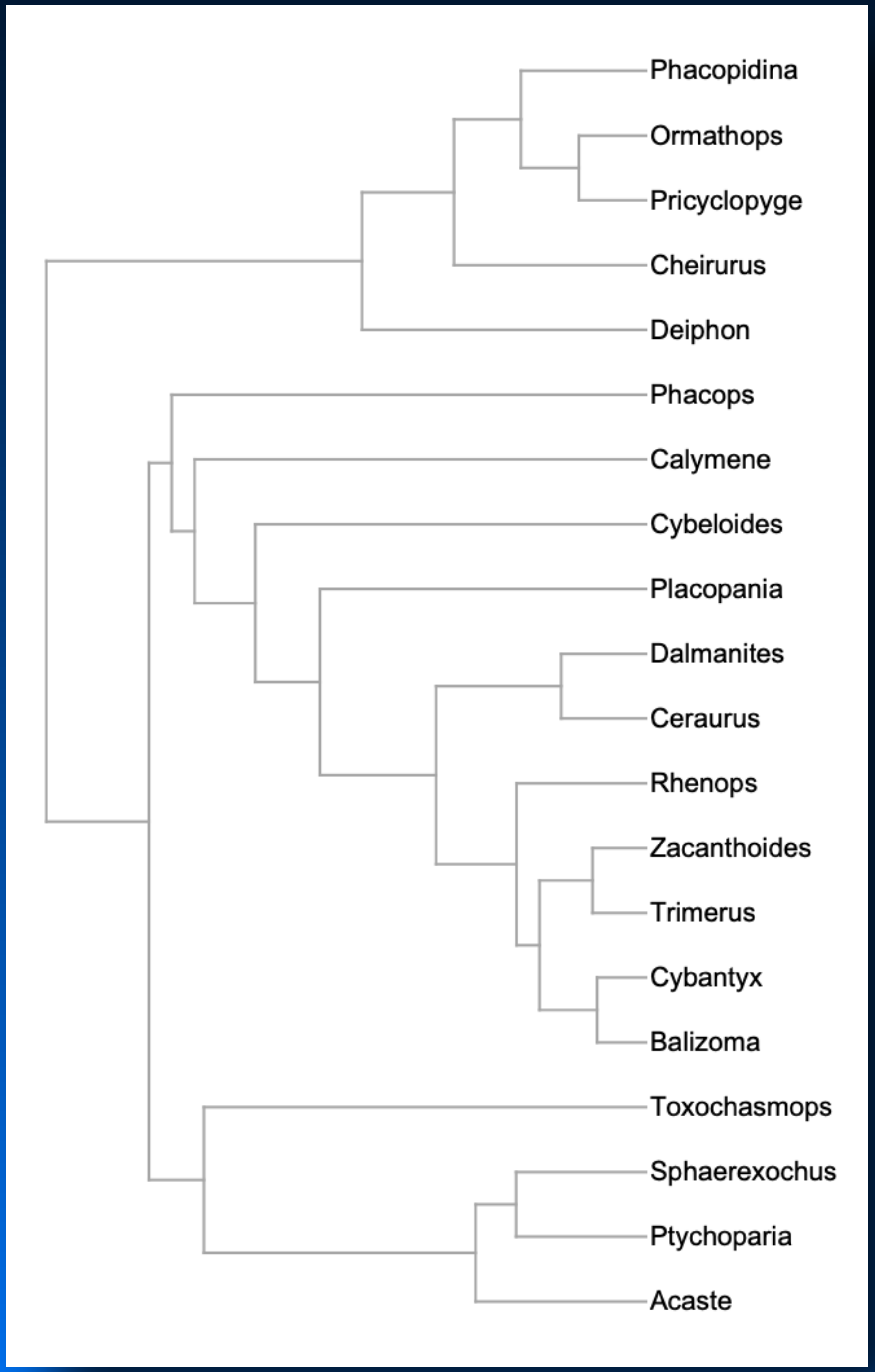
Phenetic Systematics

Advantages

- Ability to integrate data from different sources objectively.
- Ability to automate many of the processes undertaken by evolutionary systematists.
- Ability to undertake large-scale analysis by using the computers.
- Ability to extend the scope and sensitivity of data analysis over that which can be achieved by humans using qualitative and narrative methods.
- Ability to take advantage of statistical hypothesis-testing procedures
- Need to assemble a data matrix for analysis improves taxon descriptions.

Disadvantages

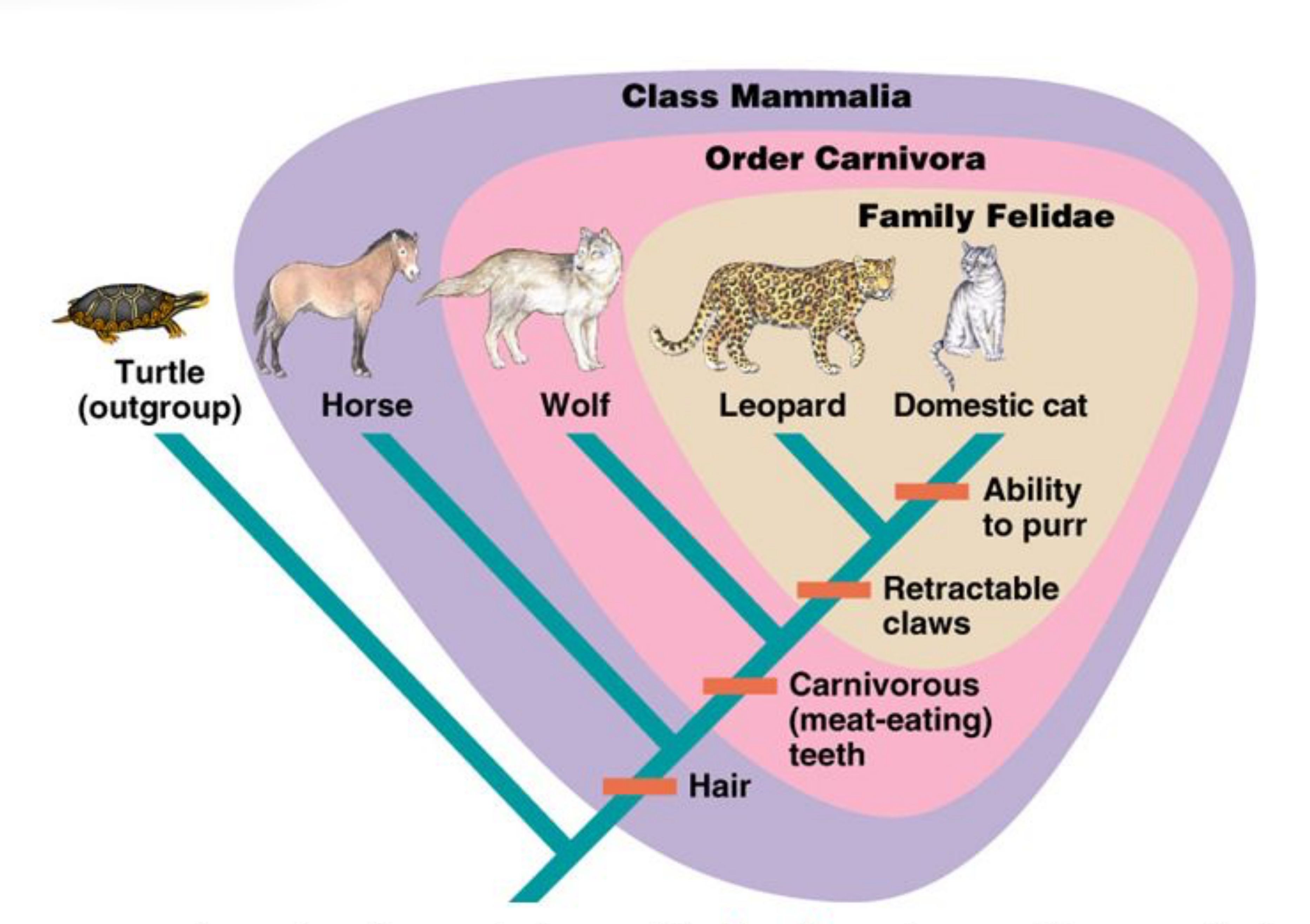
- Inconsistency of results produced by different ordination/clustering methods.
- Inconsistency of results produced by different characters collected from different parts and/or life history states of the same set of taxa.
- No distinction between monophyletic, paraphyletic and polyphyletic groups.



Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematics

Phylogenetic systematics represents a refinement of numerical taxonomy in the context of inferring phylogenetic relations via recognition that only one subset of characters carries the phylogenetic signal: characters that had been transformed from previous states by natural selection and were shared across multiple species. These are referred to as “shared, derived characters” or synapomorphies” and they are the characters that define monophyletic groups. Phylogenetic systematics uses computer search methods to find suites of synapomorphies in a character-state data matrix and evaluates the strength of empirical support for recognizing a group of species as an phylogenetically cohesive unit based on the number of co-occurring synapomorphies those species exhibit.

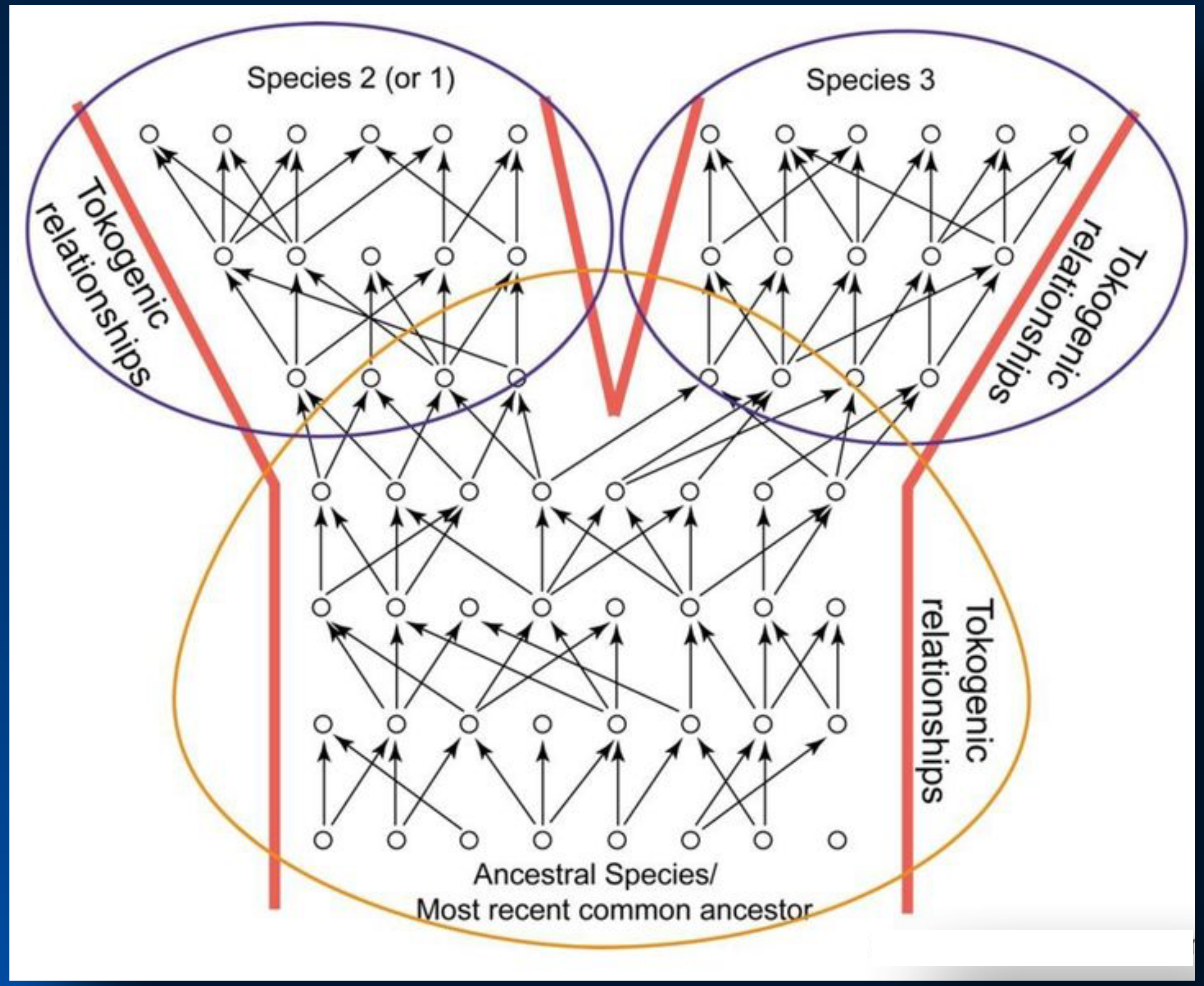


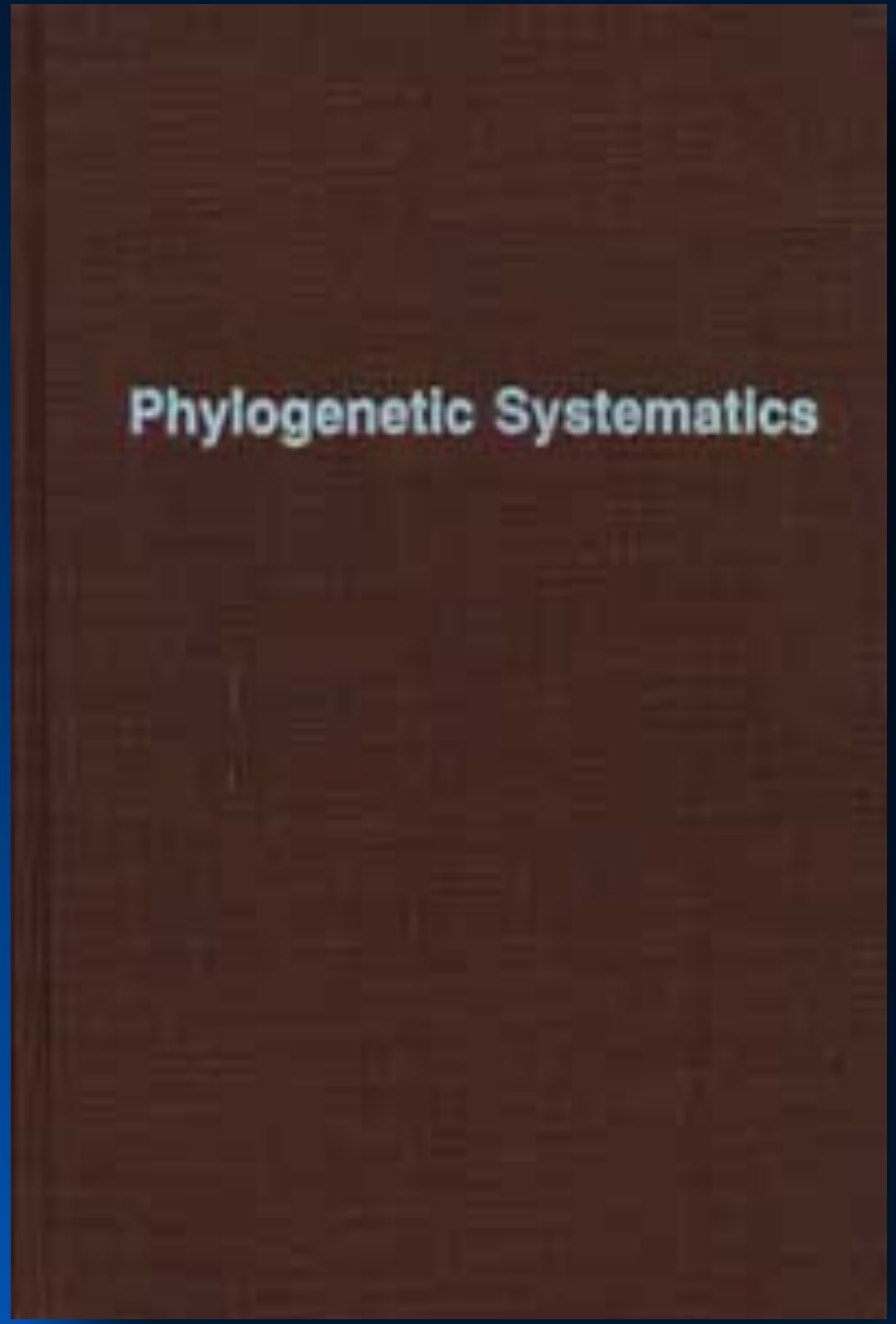
This approach to indexing phylogenetic relations is generally regarded as the most valid. However, the data are often unable to resolve relations completely and it produces an unwieldy number of classes.

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematics

Willi Hennig
(1913 – 1976)





Hennig, W., 1966, Phylogenetic systematics:
Urbana, Illinois, University of Illinois Press, 263 p.

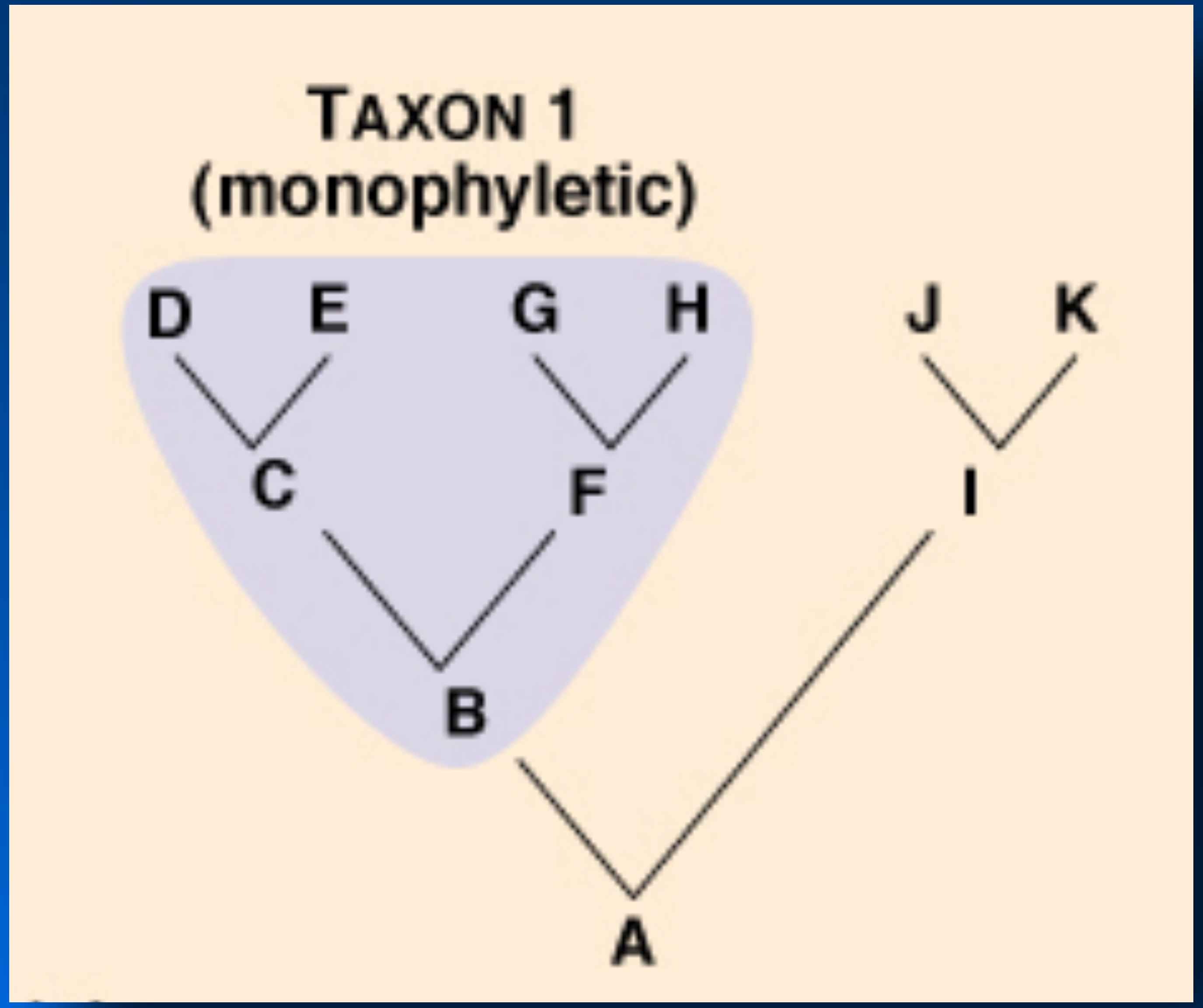
As with numerical taxonomy, many people contributed to the advancement of phylogenetic systematics. But the universally acknowledged founder of this approach was the German entomologist Willi Hennig who was among the first to advocate use of synapomorphies to trace phylogenetic relations.

Phylogenetics, Cladistics & Phylogeny

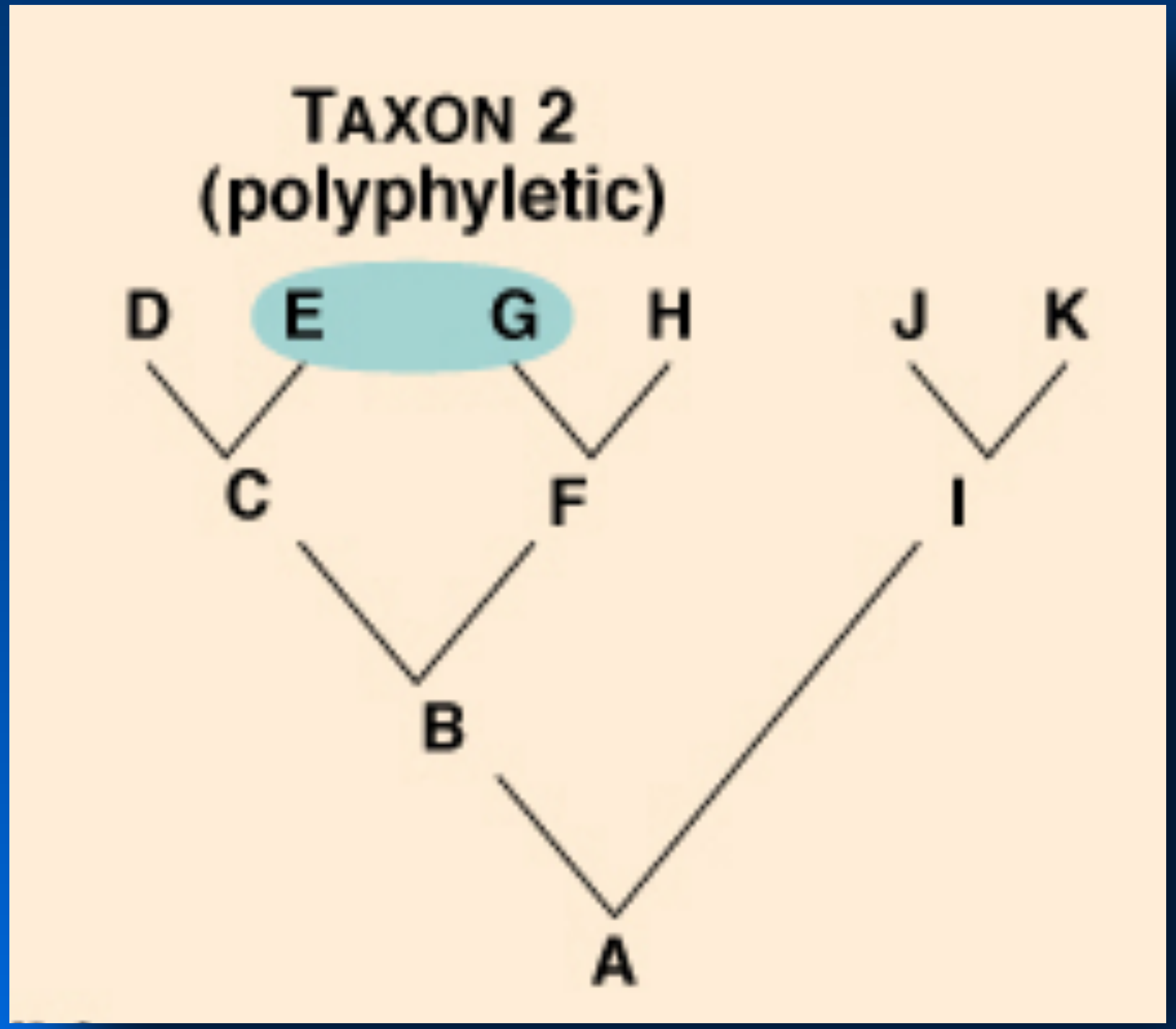
Phylogenetic Systematics

Clade - a monophyletic group of organisms composed of the common ancestor of all descendant species and all of that ancestor's descendants.

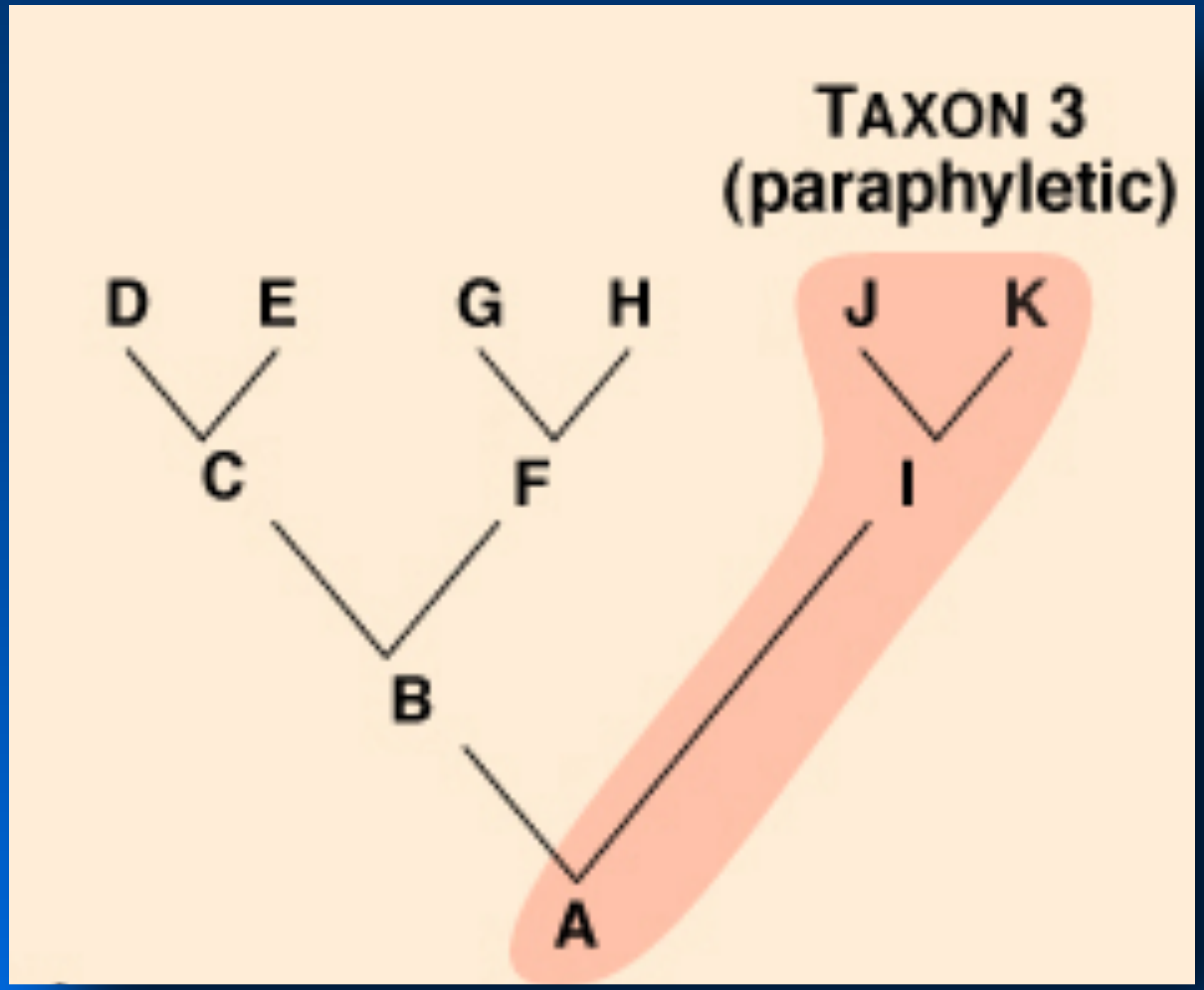
Grade - a group of organisms distinguished by a set of morphological, molecular, ecological and/or behavioral characteristics that are not unique to that group.



Clade



Grade



Grade

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematic Characters

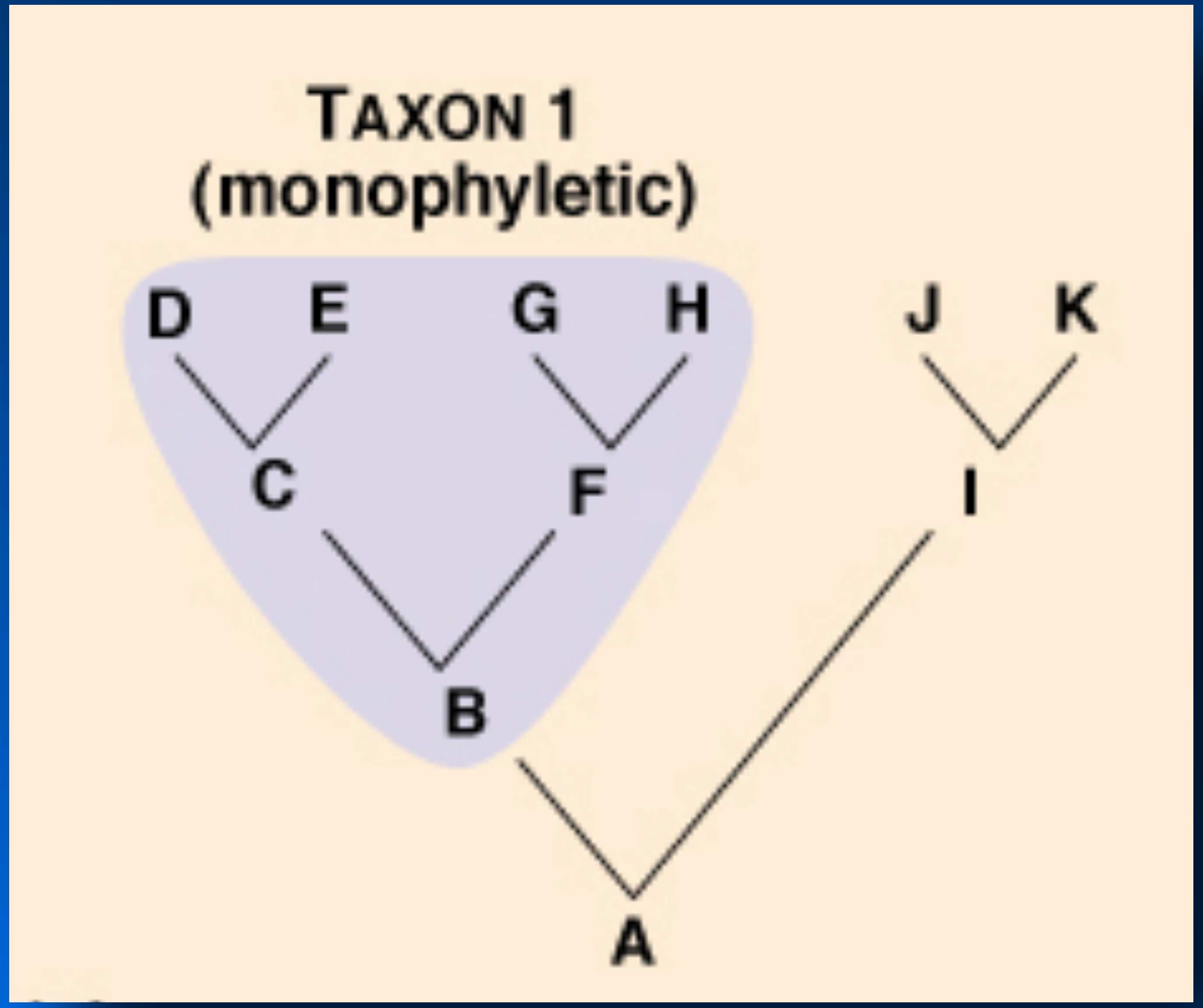
- **Apomorphy** - a novel trait or character that is unique to a particular group of phylogenetically related species.
- **Synapomorphy** - a novel trait or character that is shared by a group of phylogenetically related species.
- **Plesimorphy** - a trait or character that is not unique to a group of phylogenetically related species but may arise due to mis-identification and/or convergent evolution.
- **Synplesimorphy** - a non-unique trait or character that is shared between groups of species.
- **Autapomorphy** - a novel trait or character that is unique to a species and, so allows the species to be identified unambiguously.

Phylogenetics, Cladistics & Phylogeny

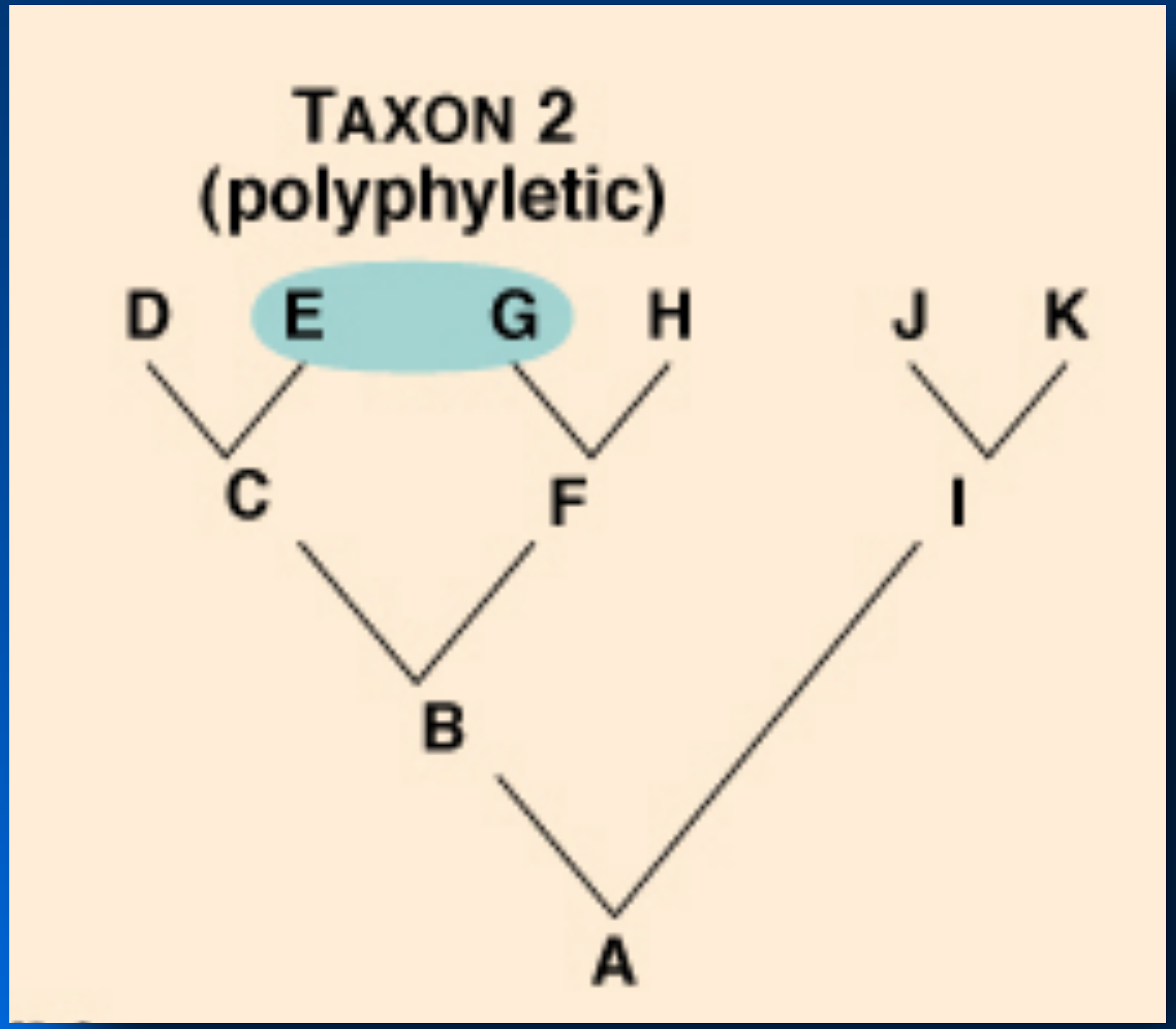
Phylogenetic Systematics

Clade - a monophyletic group of organisms composed of the common ancestor of all descendant species and all of that ancestor’s descendants.

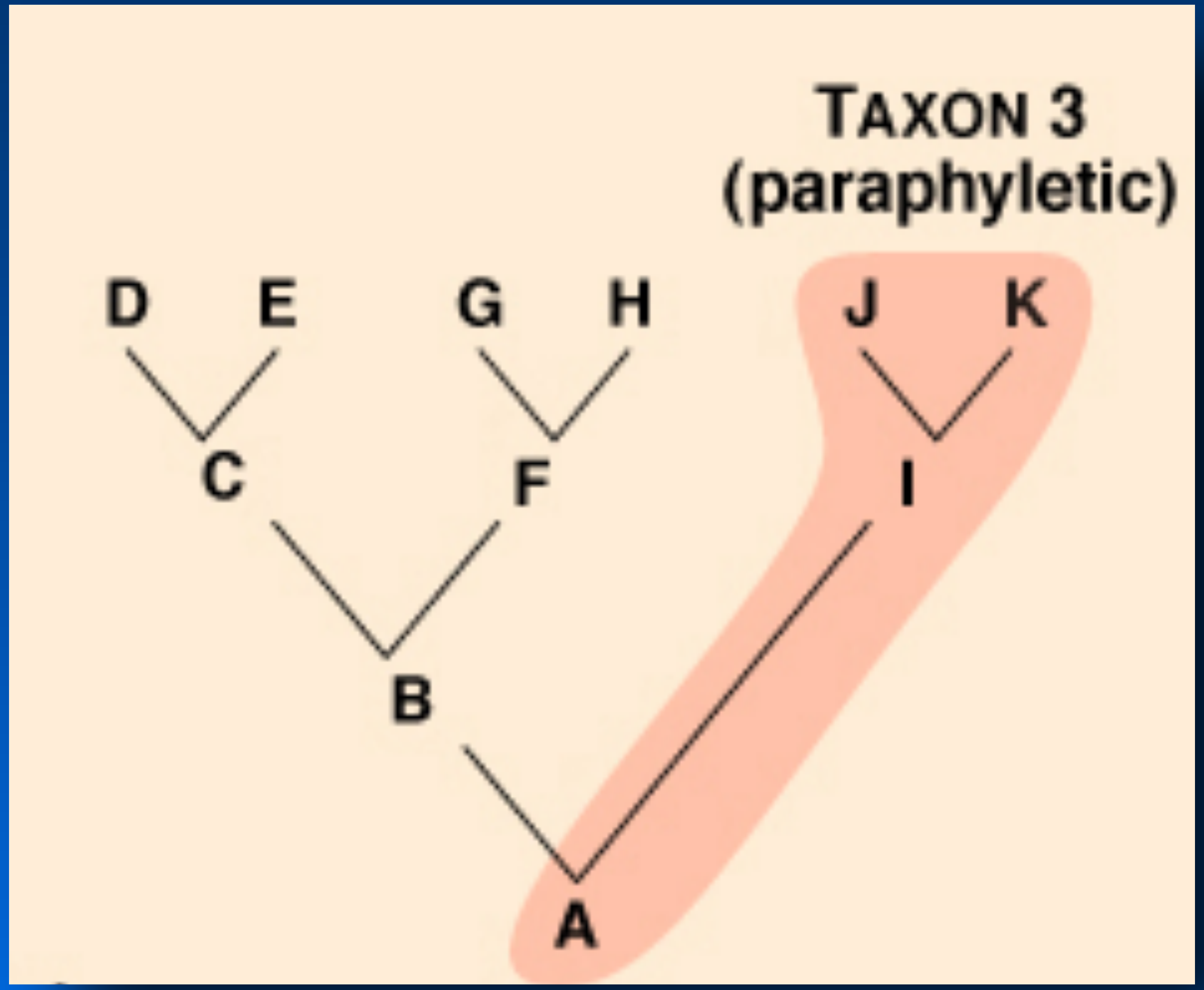
Grade - a paraphyletic or polyphyletic group of organisms distinguished by a set of morphological, molecular, ecological and/or behavioral characteristics that are not unique to that group.



Synaopomorphy



Synplesiomorphy



Synplesiomorphy

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Phylogenetic Systematics: Characters

	Character																					
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	11
A										1	1	1										
B										1			1				1		1			
C	1				1					1							1		1	1		
D	1									1						1	1		1	1		
E	1		1							1							1	1	1	1		
F		1								1				1	1		1		1			
G			1					1		1				1	1		1		1			
H									1	1				1	1		1		1			
I						1				1		1									1	1
J							1			1		1									1	1
K				1						1		1									1	1

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Phylogenetic Systematics: Autapomorphies

	Character																					
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	11
A										1	1	1										
B										1			1				1		1			
C	1				1					1							1		1	1		
D	1									1						1	1		1	1		
E	1		1							1							1	1	1	1		
F		1								1				1	1		1		1			
G			1					1		1				1	1		1		1			
H									1	1				1	1		1		1			
I						1				1		1									1	1
J							1			1		1									1	1
K				1						1		1									1	1

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Phylogenetic Systematics: Autapomorphies

	Character																				
Species	1	3	10	12	14	15	17	19	20	21	22	11	13	5	16	18	2	8	9	6	7	4
A			1	1								1										
B			1				1	1					1									
C	1		1				1	1	1					1								
D	1		1				1	1	1						1							
E	1	1	1				1	1	1							1						
F			1		1	1	1	1									1					
G		1	1		1	1	1	1										1				
H			1		1	1	1	1											1			
I			1	1						1	1									1		
J			1	1						1	1										1	
K			1	1						1	1											1

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Phylogenetic Systematics: Synapomorphies

	Character																				
Species	1	3	10	12	14	15	17	19	20	21	22	11	13	5	16	18	2	8	9	6	7	4
A			1	1								1										
B			1				1	1					1									
C	1		1				1	1	1					1								
D	1		1				1	1	1						1							
E	1	1	1				1	1	1							1						
F			1		1	1	1	1									1					
G		1	1		1	1	1	1										1				
H			1		1	1	1	1											1			
I			1	1						1	1									1		
J			1	1						1	1										1	
K			1	1						1	1											1

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Phylogenetic Systematics: Synapomorphies

	Character																					
Species	10	17	19	1	20	14	15	21	22	3	12	11	13	5	16	18	2	8	9	6	7	4
A	1										1	1										
B	1	1	1										1									
C	1	1	1	1	1									1								
D	1	1	1	1	1										1							
E	1	1	1	1	1					1						1						
F	1	1	1			1	1										1					
G	1	1	1			1	1			1								1				
H	1	1	1			1	1												1			
I	1							1	1		1									1		
J	1							1	1		1										1	
K	1							1	1		1											1

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Phylogenetic Systematics: Synplesiomorphies

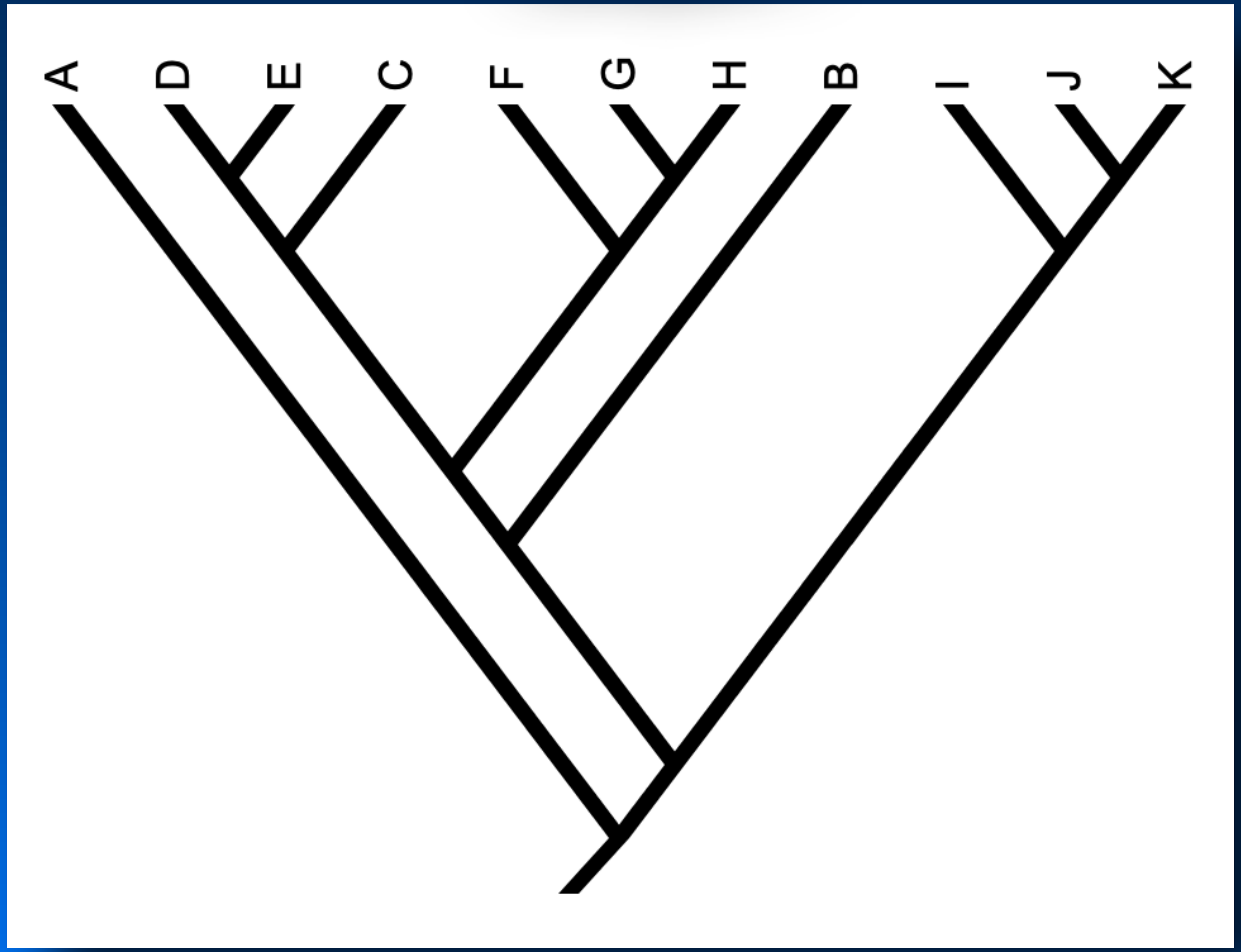
	Character																					
Species	10	17	19	1	20	14	15	21	22	3	12	11	13	5	16	18	2	8	9	6	7	4
A	1										1	1										
B	1	1	1										1									
C	1	1	1	1	1									1								
D	1	1	1	1	1										1							
E	1	1	1	1	1					1						1						
F	1	1	1			1	1										1					
G	1	1	1			1	1			1								1				
H	1	1	1			1	1												1			
I	1							1	1		1									1		
J	1							1	1		1										1	
K	1							1	1		1											1

Phylogenetics, Cladistics & Phylogeny

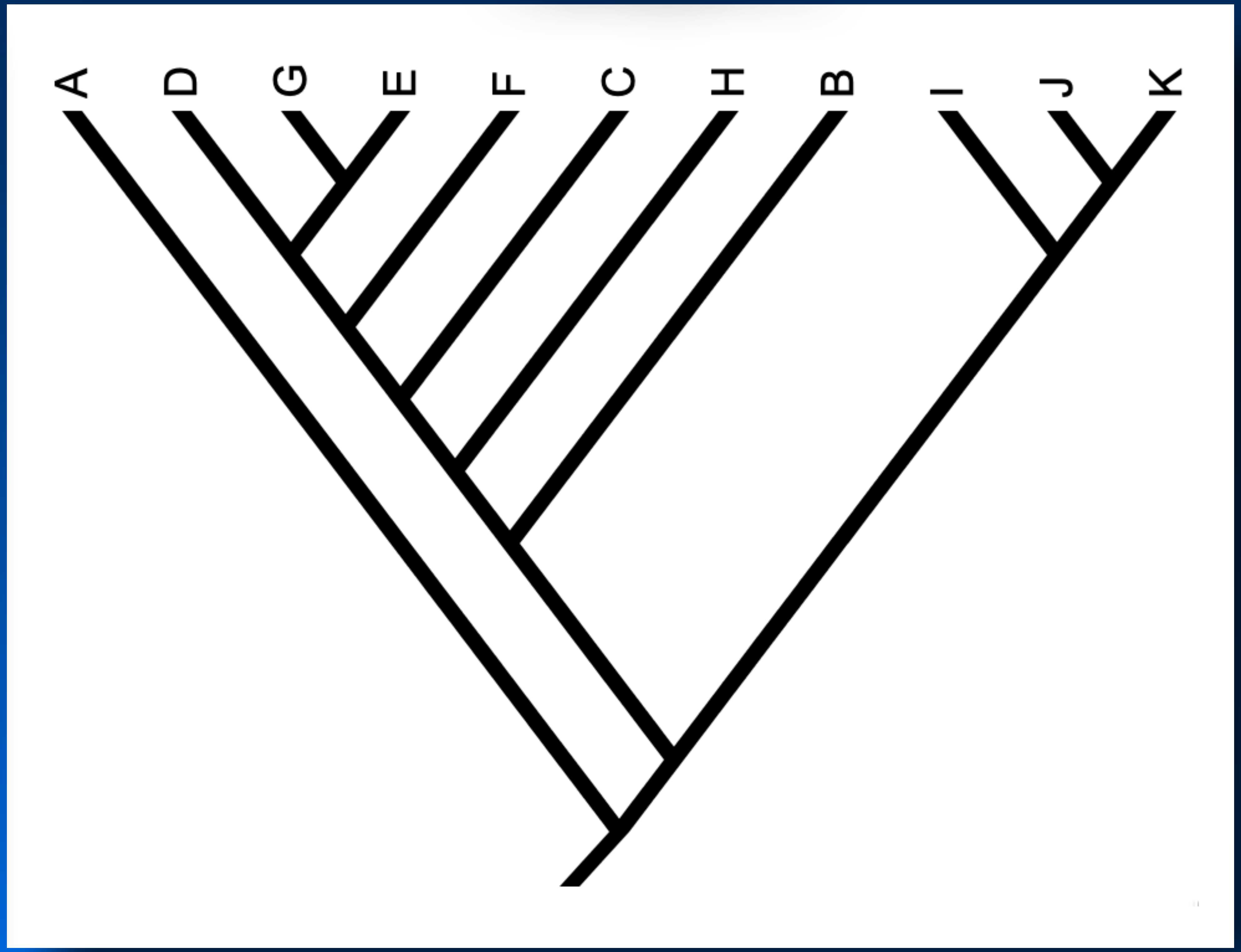
Phylogenetic Systematic Trees

How can we decide which pattern of phylogenetic relations is "better" (= has the most empirical support)?

Cladogram 1



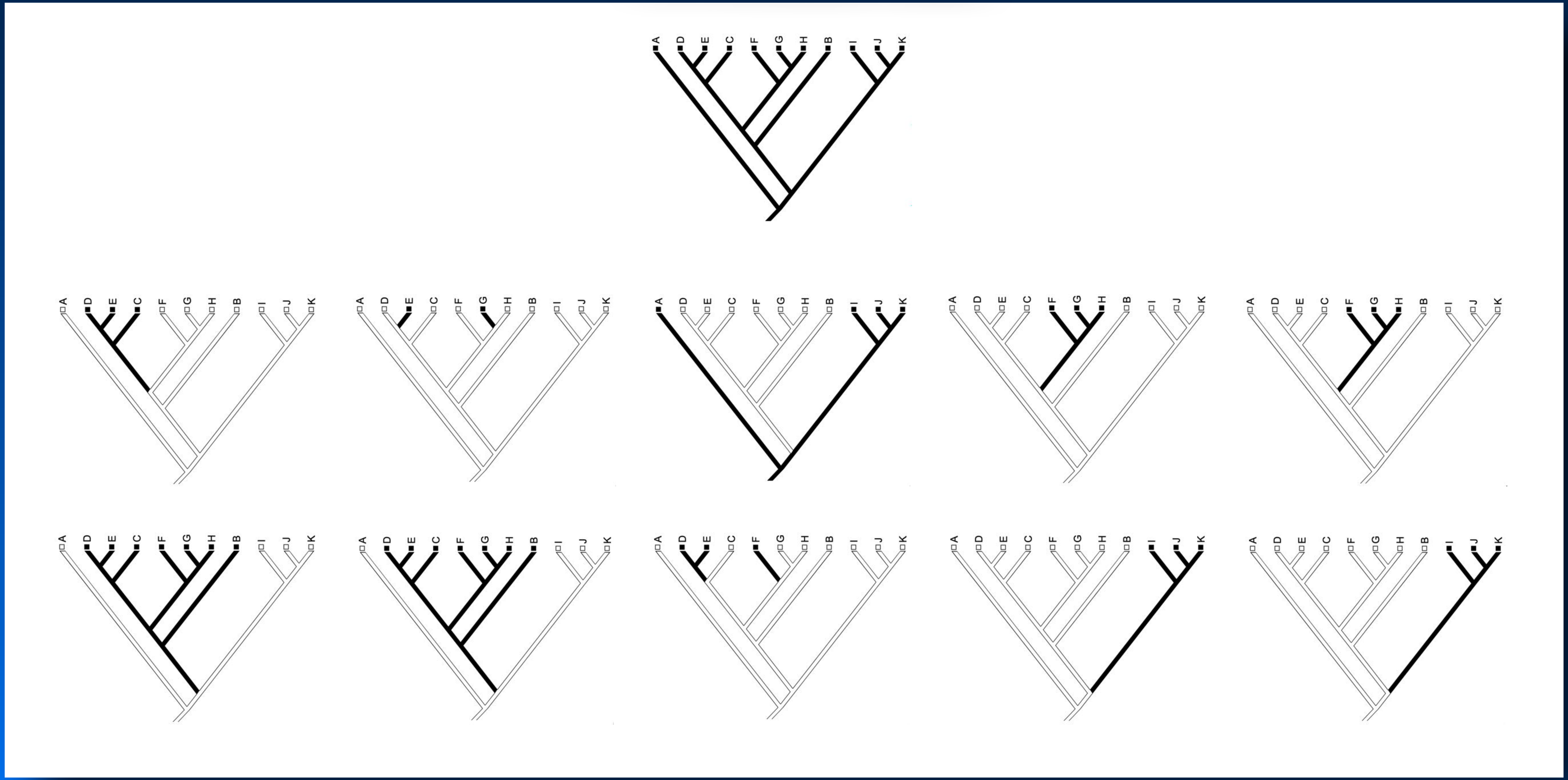
Cladogram 2



Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematic Inference

Parsimony - The principle that favors they hypothesis which exhibits the greatest degree of consistency with the available data.



Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematic Inference

Parsimony - The principle that favors they hypothesis which exhibits the greatest degree of consistency with the available data.

- **Tree length** - the number of character-state changes implied by a given tree topology (= cladogram).
- **Consistency Index** - the ratio s/m where m = the minimum number of steps a character can exhibit on any cladogram and s = the minimum number of steps implied by a given cladogram.
- **Retention Index** - the ratio $(g-s)/(g-m)$ where g = the greatest number of steps a character can exhibit over any cladogram, m = the minimum number of steps a character can exhibit on any cladogram, and s = the minimum number of steps implied by a given cladogram.

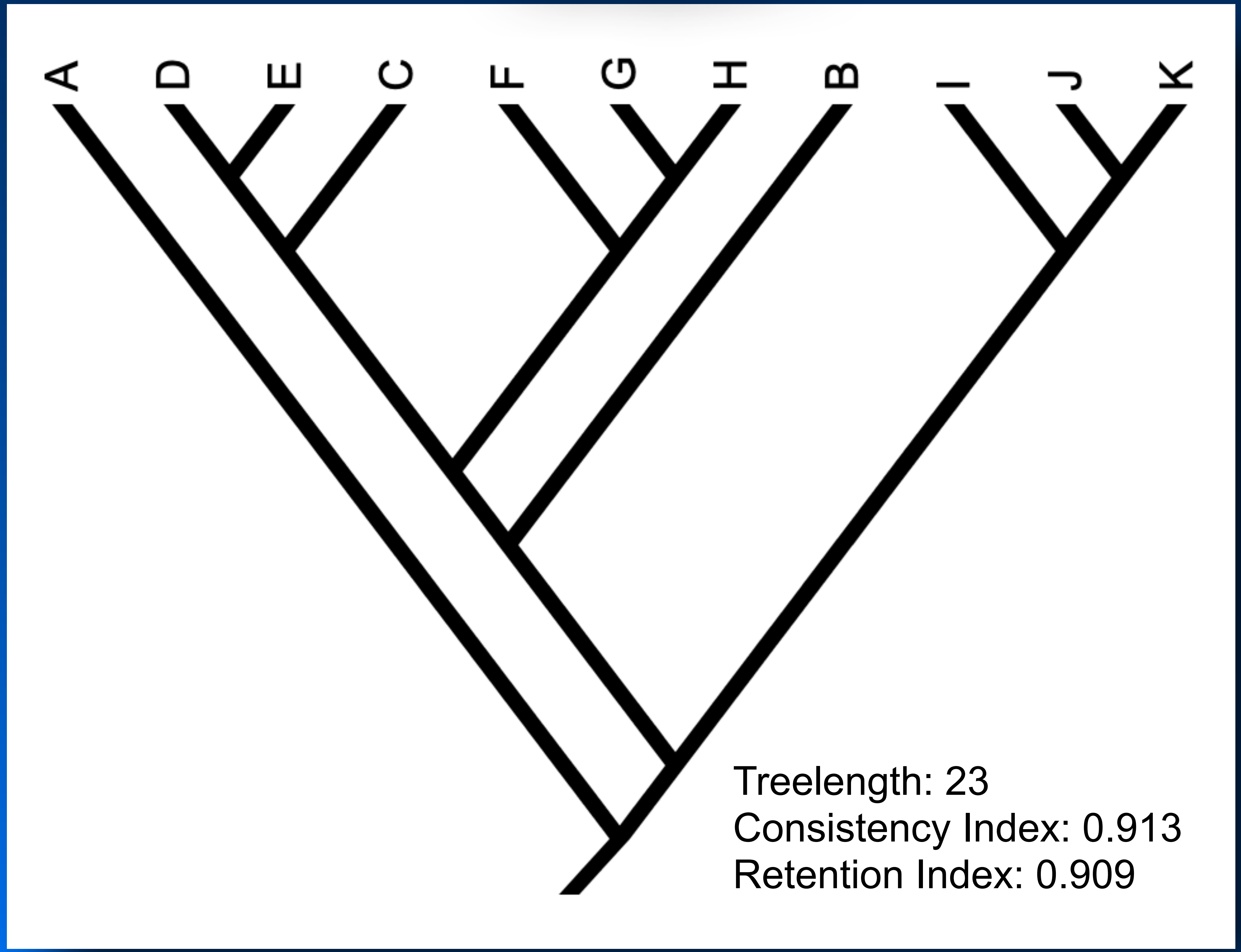
These values may be calculated for any character and summed across all characters to yield a summary for the cladogram.

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematic Trees

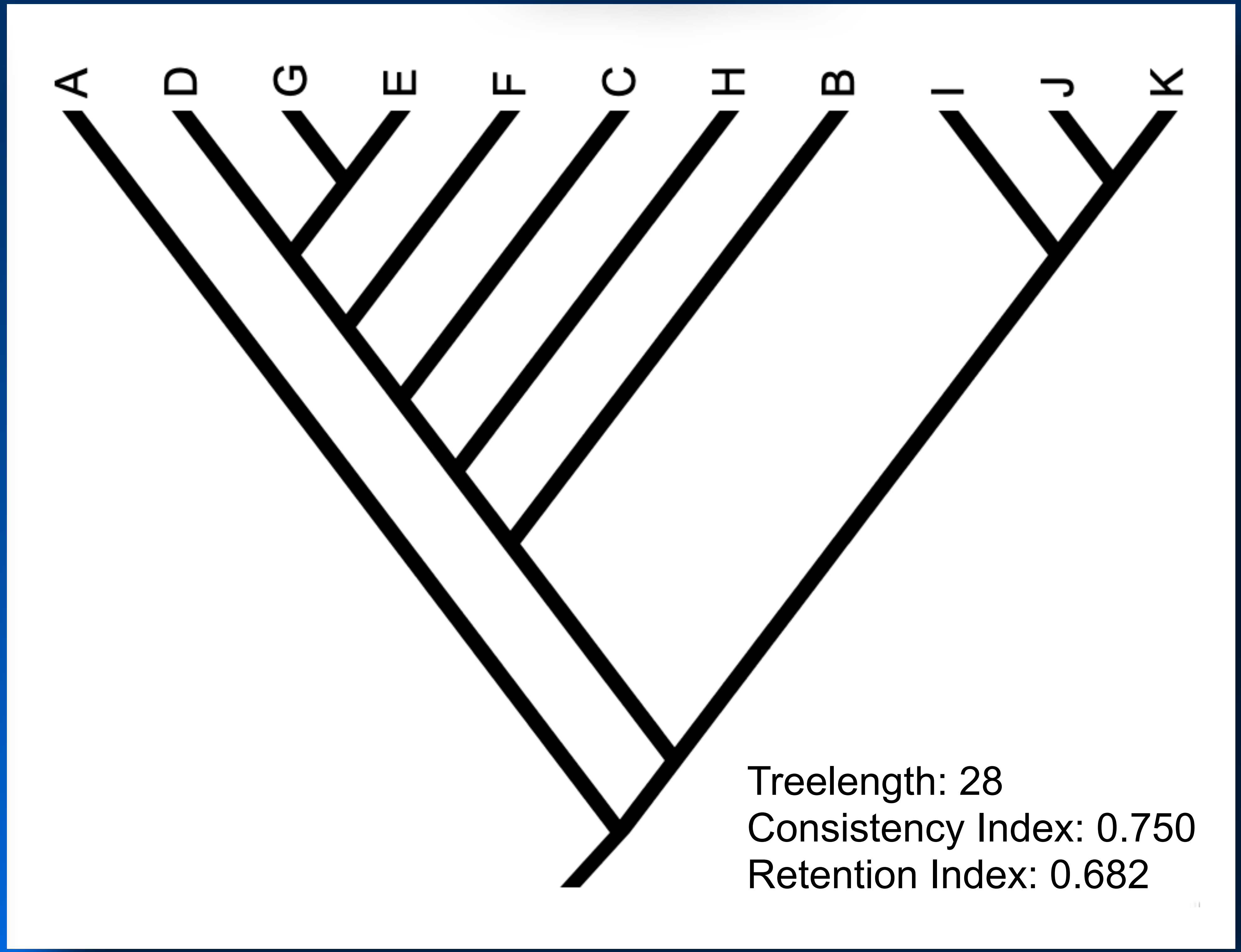
How can we decide which pattern of phylogenetic relations is “better” (= has the most empirical support)?

Cladogram 1



Treelength: 23
Consistency Index: 0.913
Retention Index: 0.909

Cladogram 2



Treelength: 28
Consistency Index: 0.750
Retention Index: 0.682

Phylogenetics, Cladistics & Phylogeny

Inferring the Pattern of Ancestry and Descent

Phylogenetic Systematics: Cladograms

Taxa	Non-Bifurcating Heirarchical topologies	Taxa	Non-Bifurcating Heirarchical topologies
1	-	11	34,459,425
2	1	12	654,729,075
3	1	13	13,749,310,575
4	3	14	316,234,143,225
5	15	15	7,905,853,580,625
6	105	16	213,458,046,676,875
7	945	17	6,190,283,353,629,380
8	10,395	18	> 191 x10^{15}
9	135,135	19	> 6,332 x 10^{15}
10	2,027,025	20	> 221,643 x 10^{15}

The complexity of phylogenetic-analysis problems more-or-less requires the use of sophisticated optimization algorithms for all but the smallest and simplest analyses.

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematic Character Polarity

Character polarization refers to the order to character state changes, especially over time, especially in the case of multi-state characters. Polarization also supports the unambiguous distinction between plesiomorphic and apomorphic character states.

- Unpolarized - All transitions between character states allowed.
- Outgroup* polarization - For a given character with two or more states within a group the state occurring in the outgroup assumed to be the plesiomorphic state.
- Ontogenetic polarization - For a given character with two or more states within a group the state appearing earlier in ontogeny is assumed to be the plesiomorphic state.

* An outgroup is a taxon from a different, but closely related, monophyletic group that is included in a phylogenetic analysis in order to establish a basis for character-state polarization.

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematic Character Polarity

Simplifying Assumptions

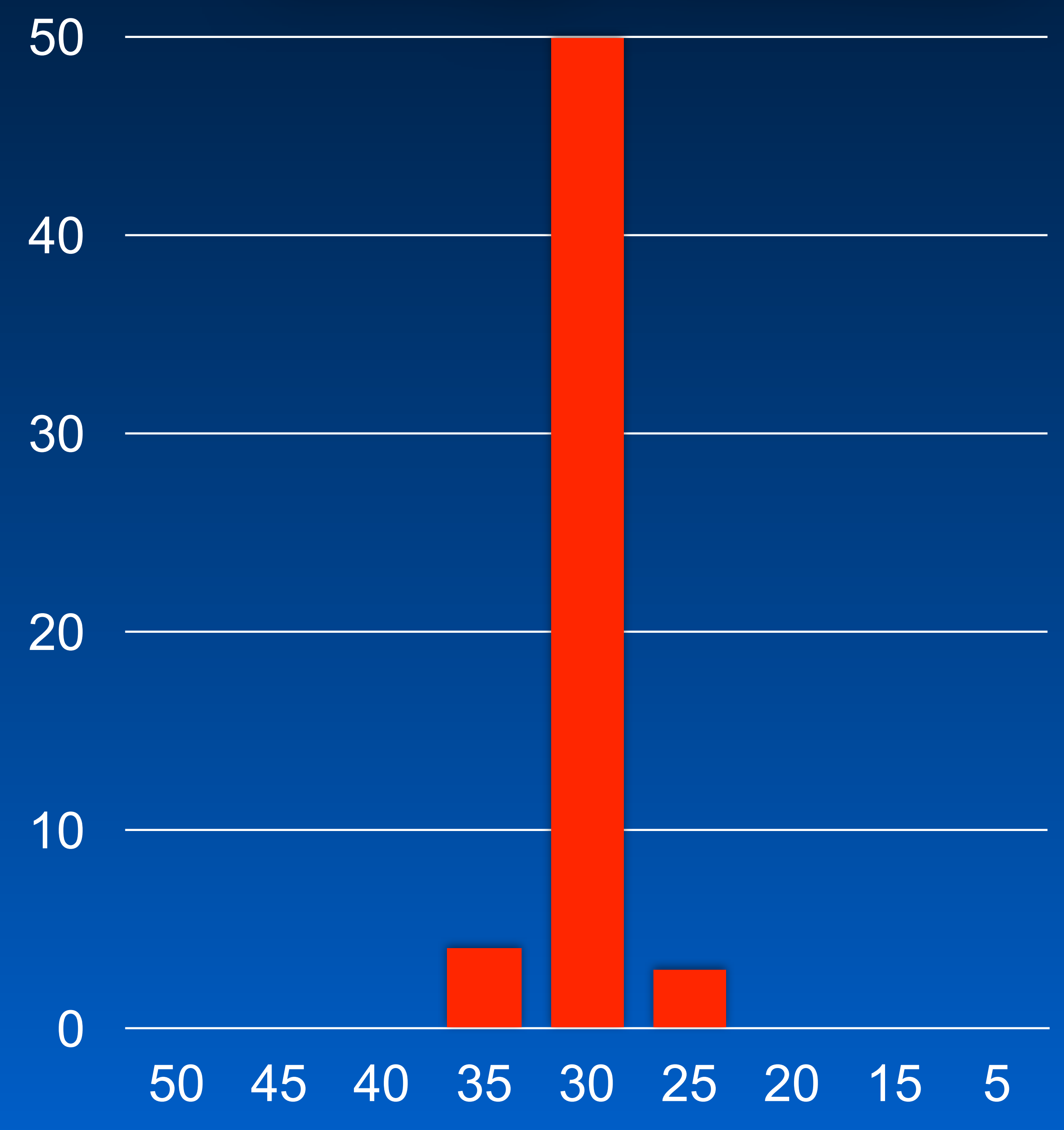
- Ingroup Commonality - the state(s) that occur(s) with the highest frequency in the ingroup can be assumed to be plesiomorphic relative to states that occur in lower frequencies.
- Stratigraphy - if one character state occurs only in older fossils, and another occurs only in younger fossils, the former can be assumed to be plesiomorphic relative to the latter.
- Biogeography - the state(s) that occur(s) with the highest geographic distribution in the ingroup can be assumed to be plesiomorphic relative to states that exhibit more restricted geographic distributions.

Note: these are all assumptions and must be evaluated on a case-by-case basis to determine whether or not their invocation is reasonable in any particular analysis.

Phylogenetics, Cladistics & Phylogeny

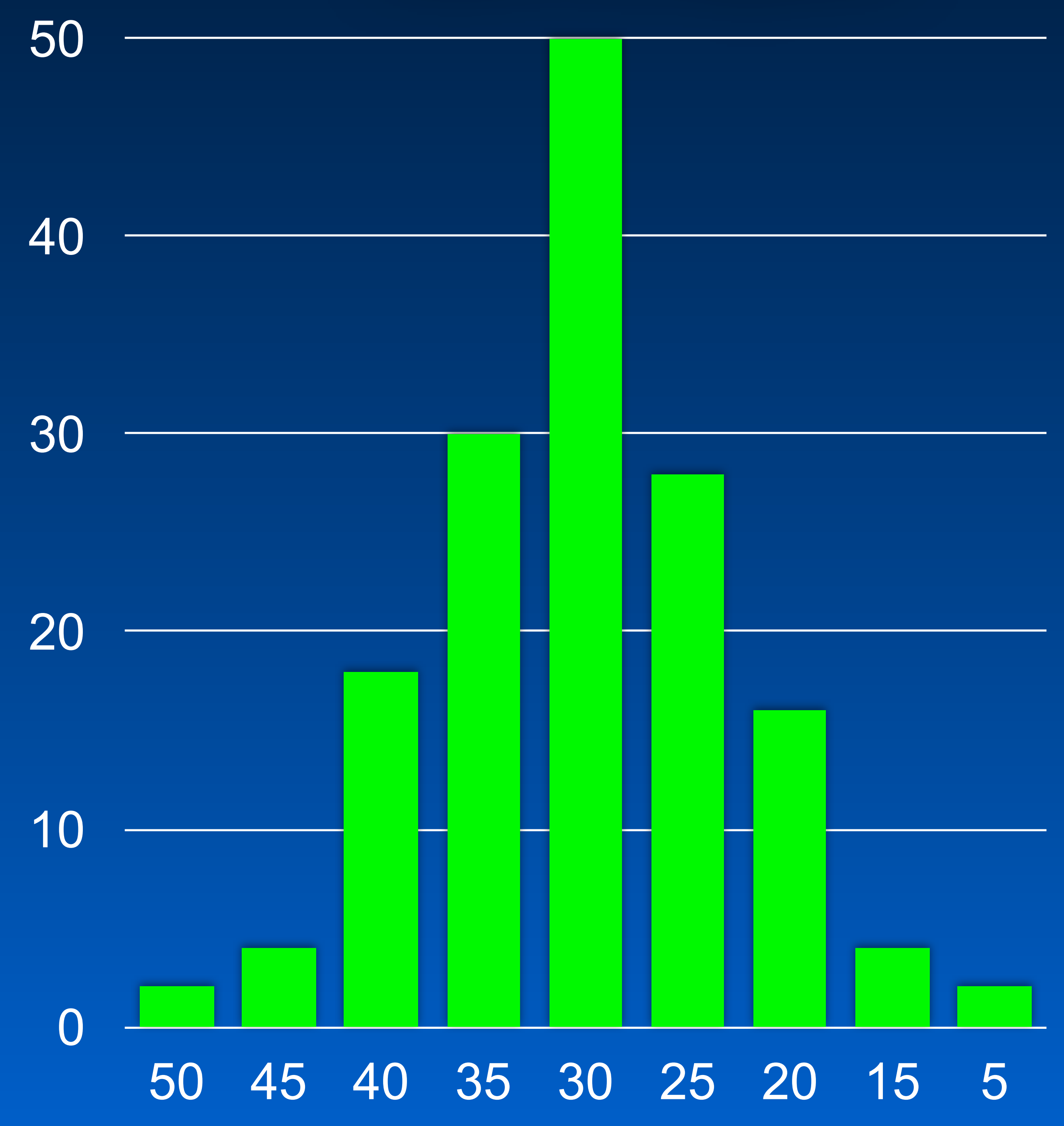
Phylogenetic Systematics: Branch-Length Distributions

Strongly Unimodal



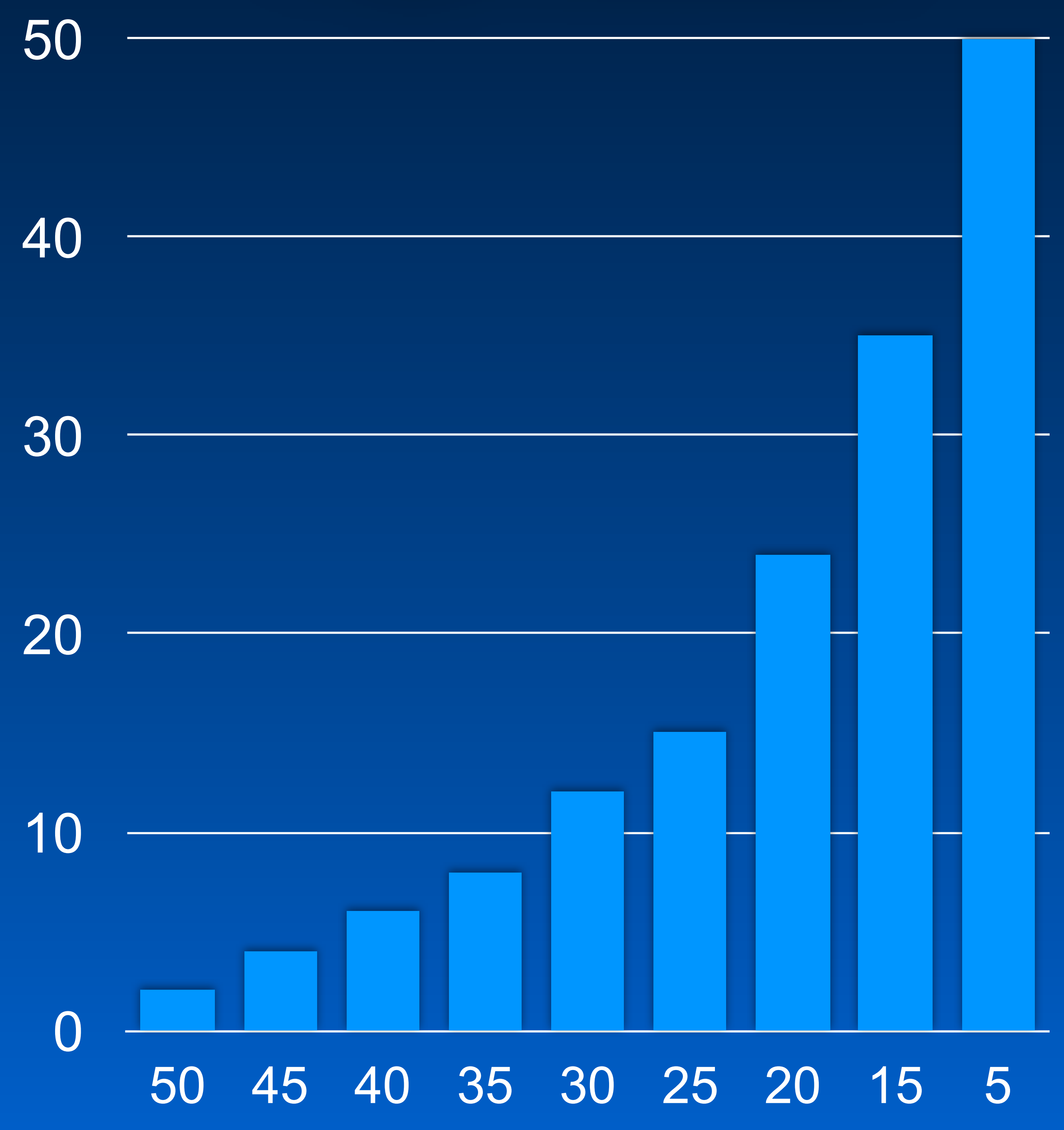
No signal & little noise; all cladograms equally parsimonious.

Bell-Shaped



Near random data; many near parsimonious, but few maximally parsimonious solutions.

Right-Skewed

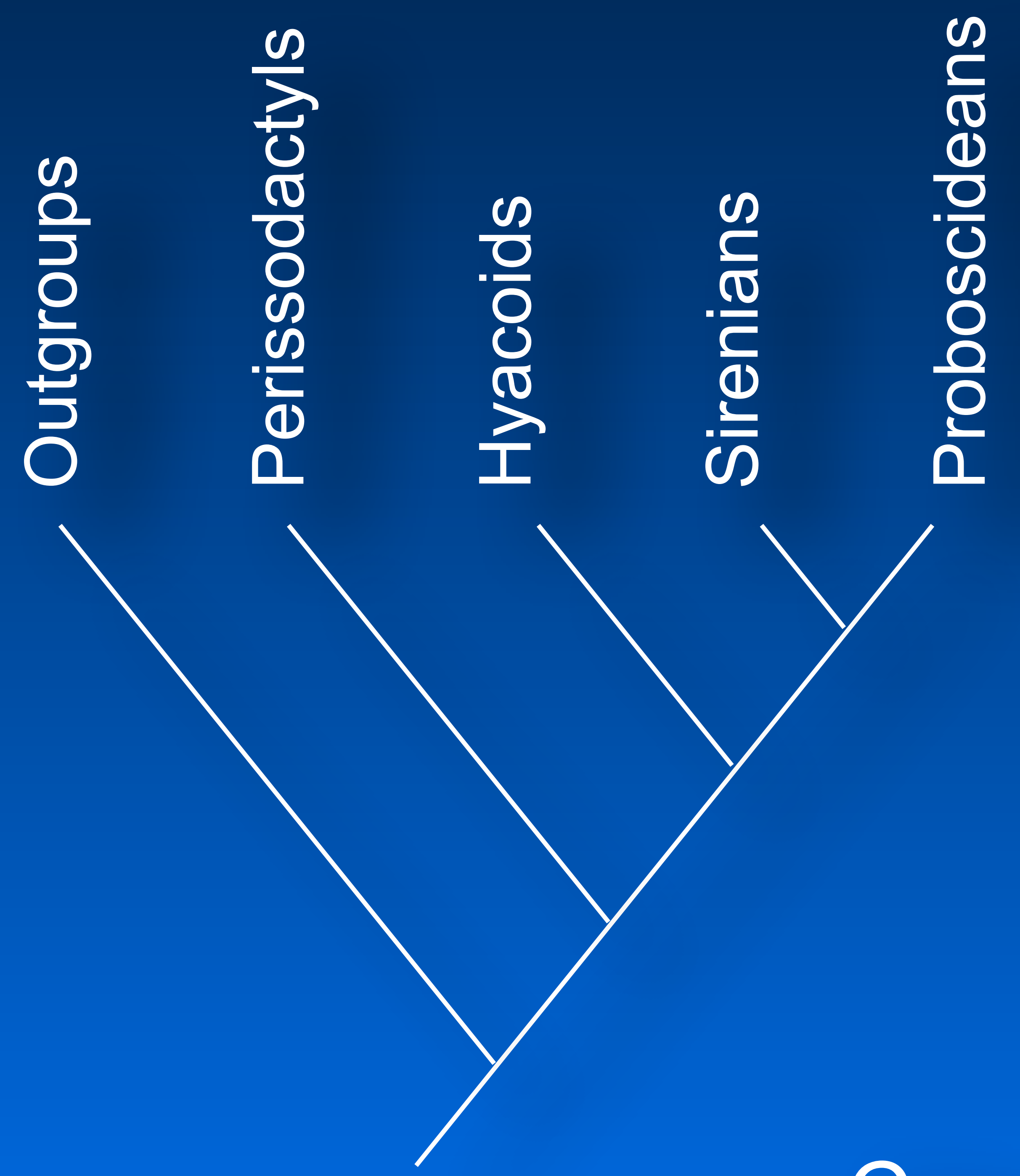


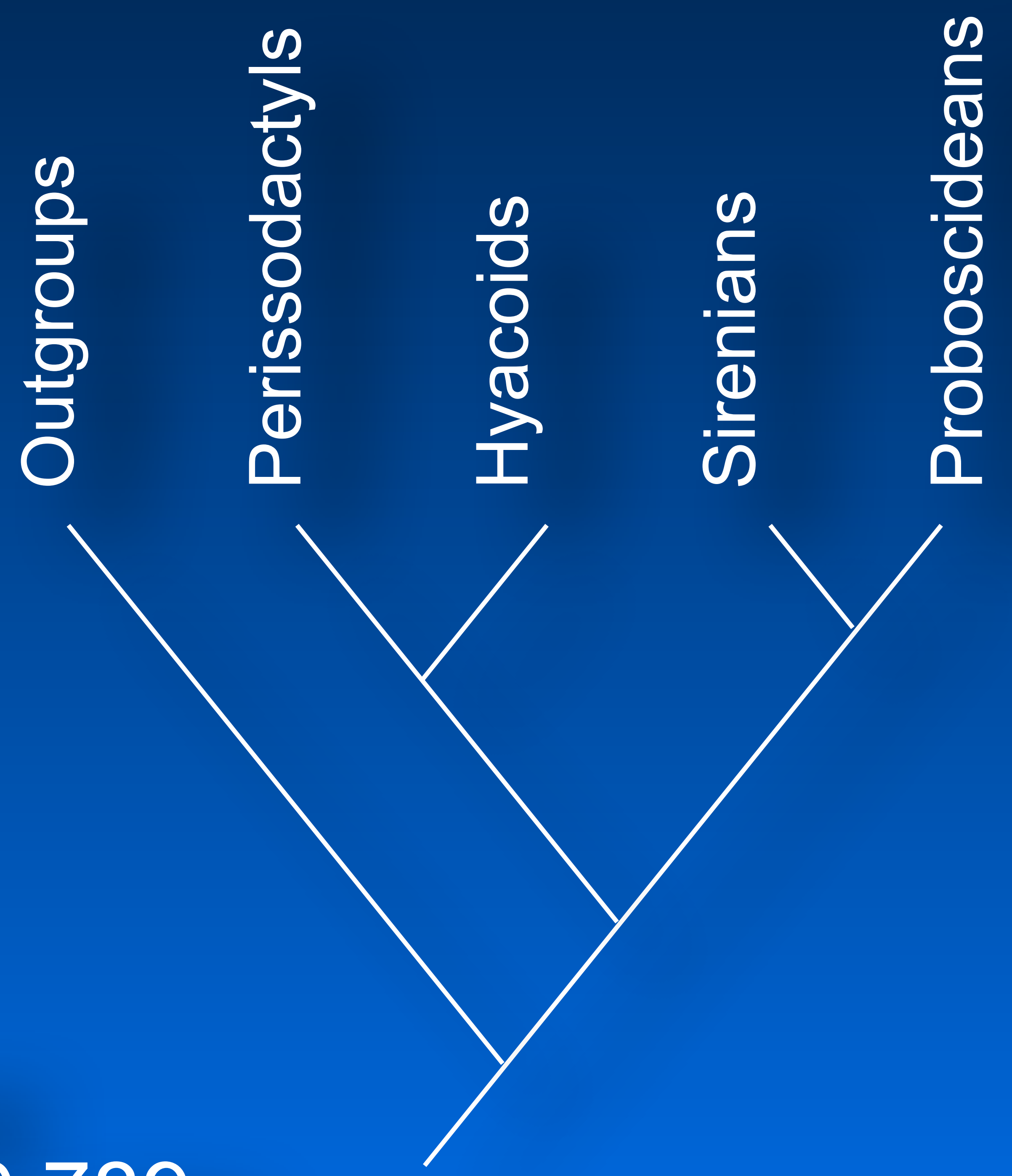
Strong signal with one or a few cladograms being more parsimonious than the rest.

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematics & Fossils

Two equally parsimonious cladograms depicting eutherian mammal phylogenetic relations based only on the character states of extant mammals.



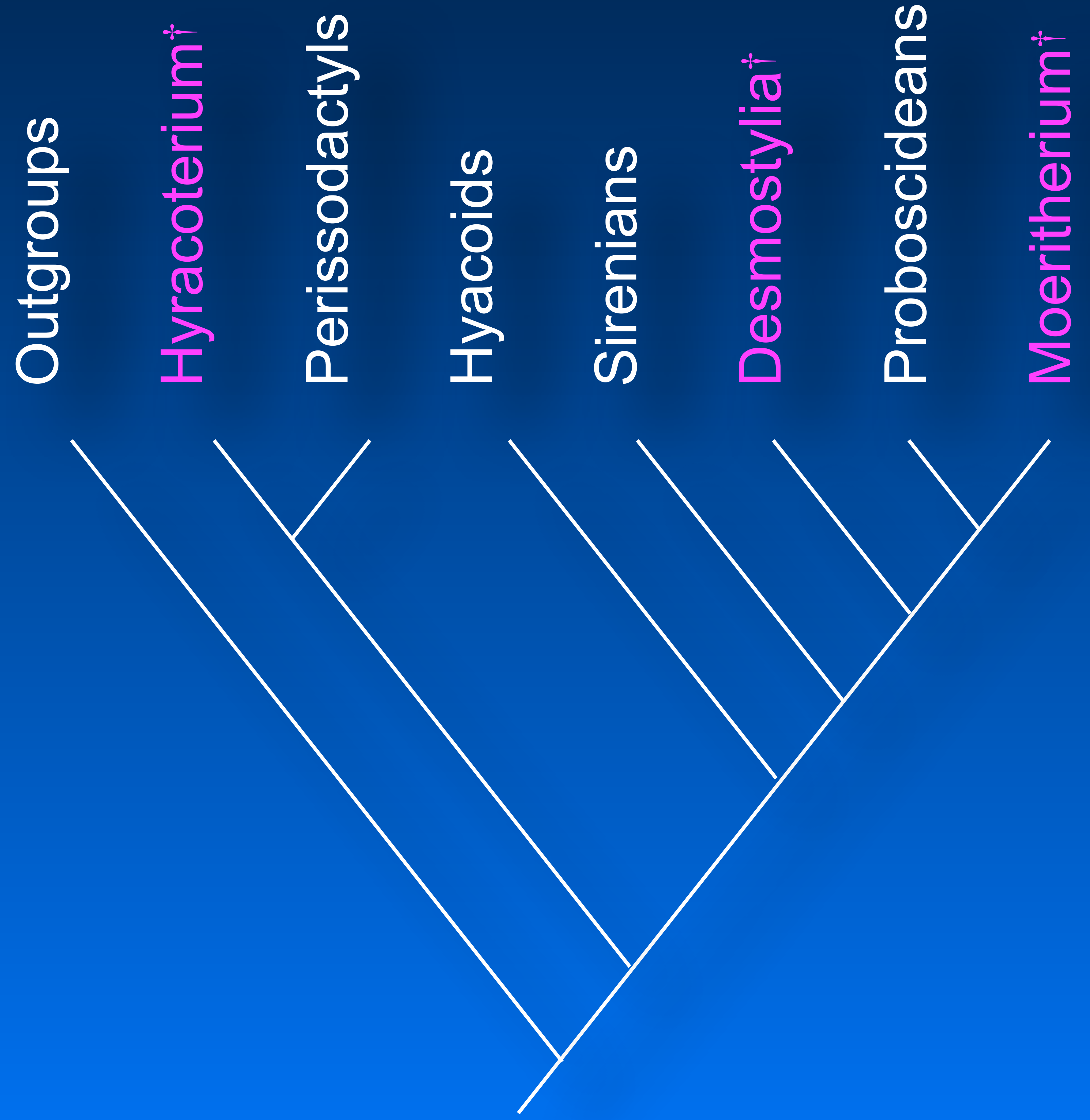


Treelength: 38
Consistency Index: 0.789
Retention Index: 0.619

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematics & Fossils

When fossil taxa are included in the analysis a single cladogram with superior quality indices results, thus clarifying eutherian mammal phylogenetic relations.



Treelength: 38
Consistency Index: 0.789
Retention Index: 0.826

* † = fossil taxon.

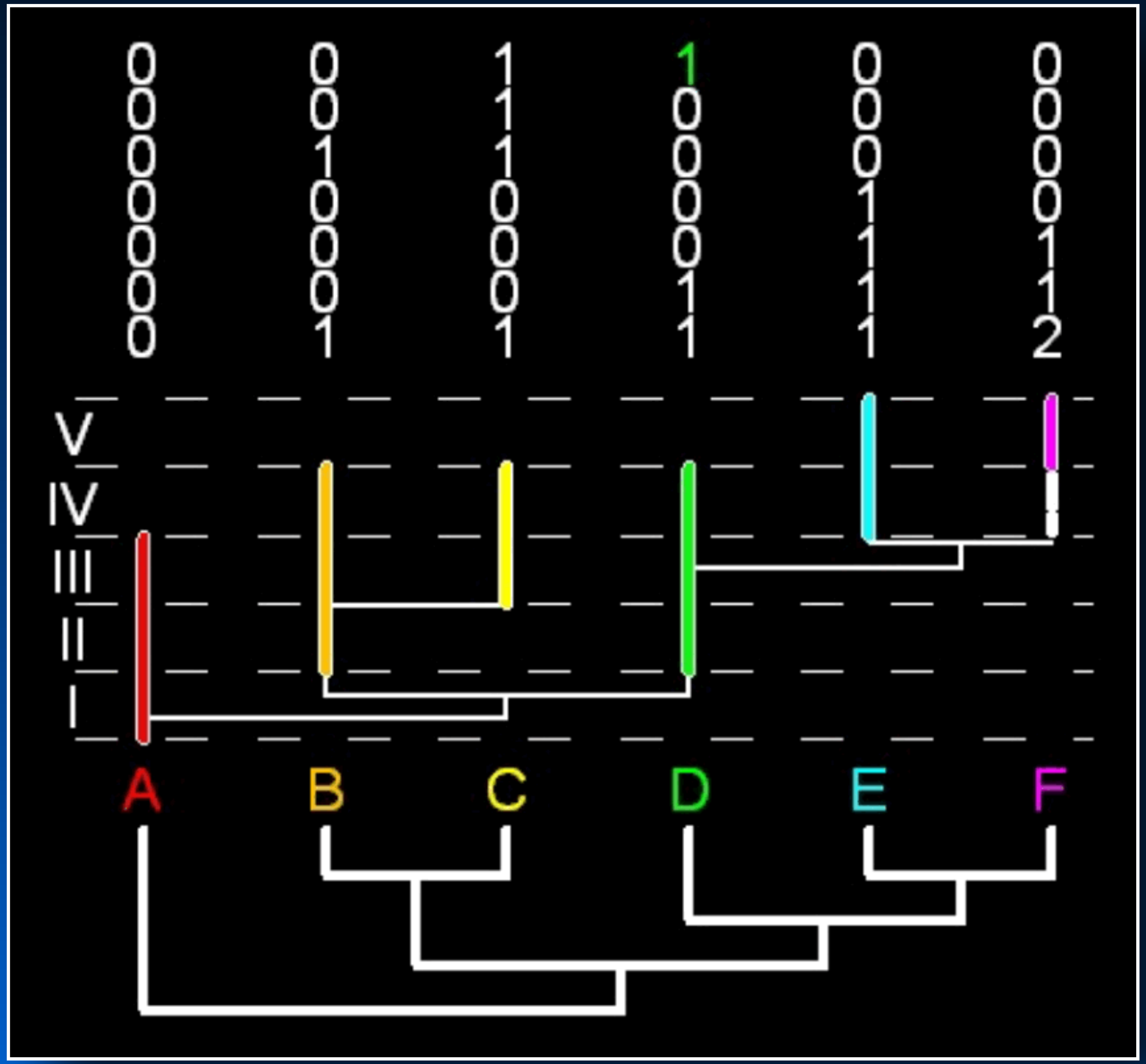
Phylogenetics, Cladistics & Phylogeny

Stratocladistics

Like stratophenetics, stratocladistics represents an attempt to include patterns of stratigraphic first appearances as criteria that could be used to infer phylogenetic relations in an overall cladistic context.

Terminal species recognized operationally as having unique apomorphies, ancestral taxa recognized as having no apomorphies.

This approach recognizes that stratigraphic data may disagree with morphological/genetic data, but proposes that all data be included in the effort to minimize incongruences.

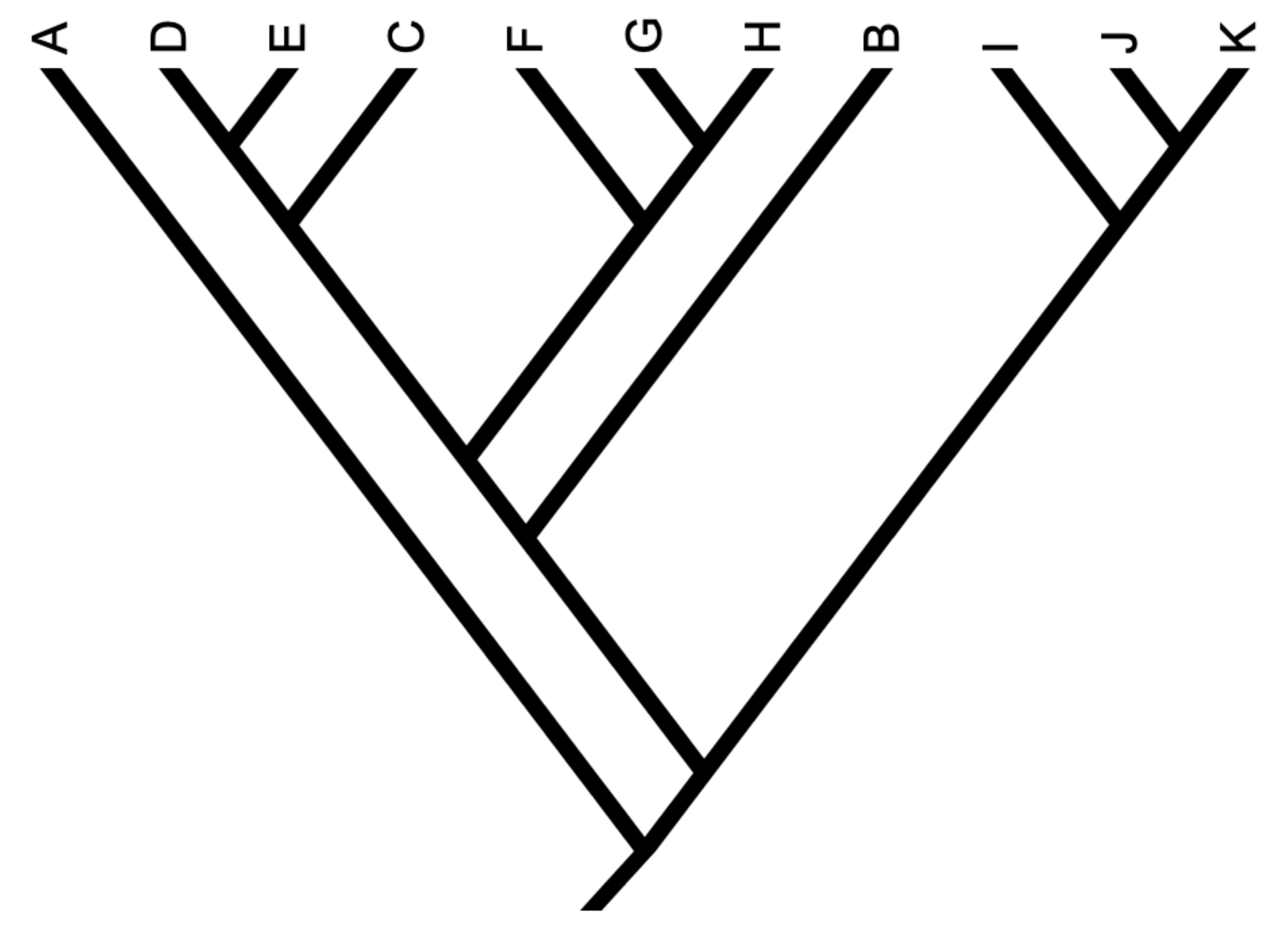


The primary difficulty lies with descisions regarding the relative scalings of morphological/genetic parsimony debt and stratigraphic parsimony debt in the overall parsimony calculation.

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematics & Ancestors

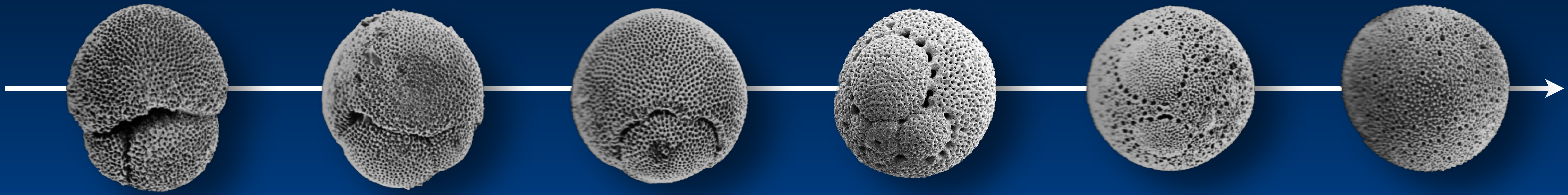
The nodes of a cladogram represent hypothetical ancestors that must exist if the cladogram is correct, but they do not represent actual ancestors in the sense of taxa there is actual evidence for. If branch lengths are accurate and an accurate model of evolutionary change is available, it is possible to use states of the terminal taxa to estimate the probable states of these hypothetical ancestors. But these estimates will only be as good as the evidence on which they are based. In accurate cladograms it is possible, in principle, to identify ancestor species: species whose morphologies are composed entirely of ancestral character states. But actual examples of ancestral species are quite rare.



Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematics & Ancestors

Examples of Ancestors



Trilobatus sicanus

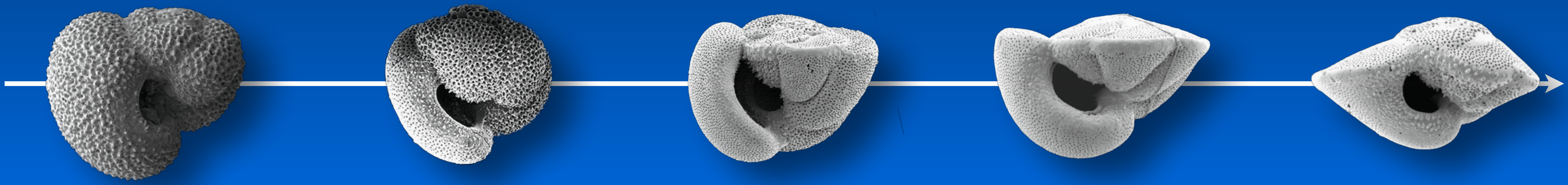
Praeorbulina curva

Praeorbulina glomerosa glomerosa

Praeorbulina glomerosa circulars

Orbulina sutralis

Orbulina Universa



Turborotalia frontosa

Turborotalia pomeroli

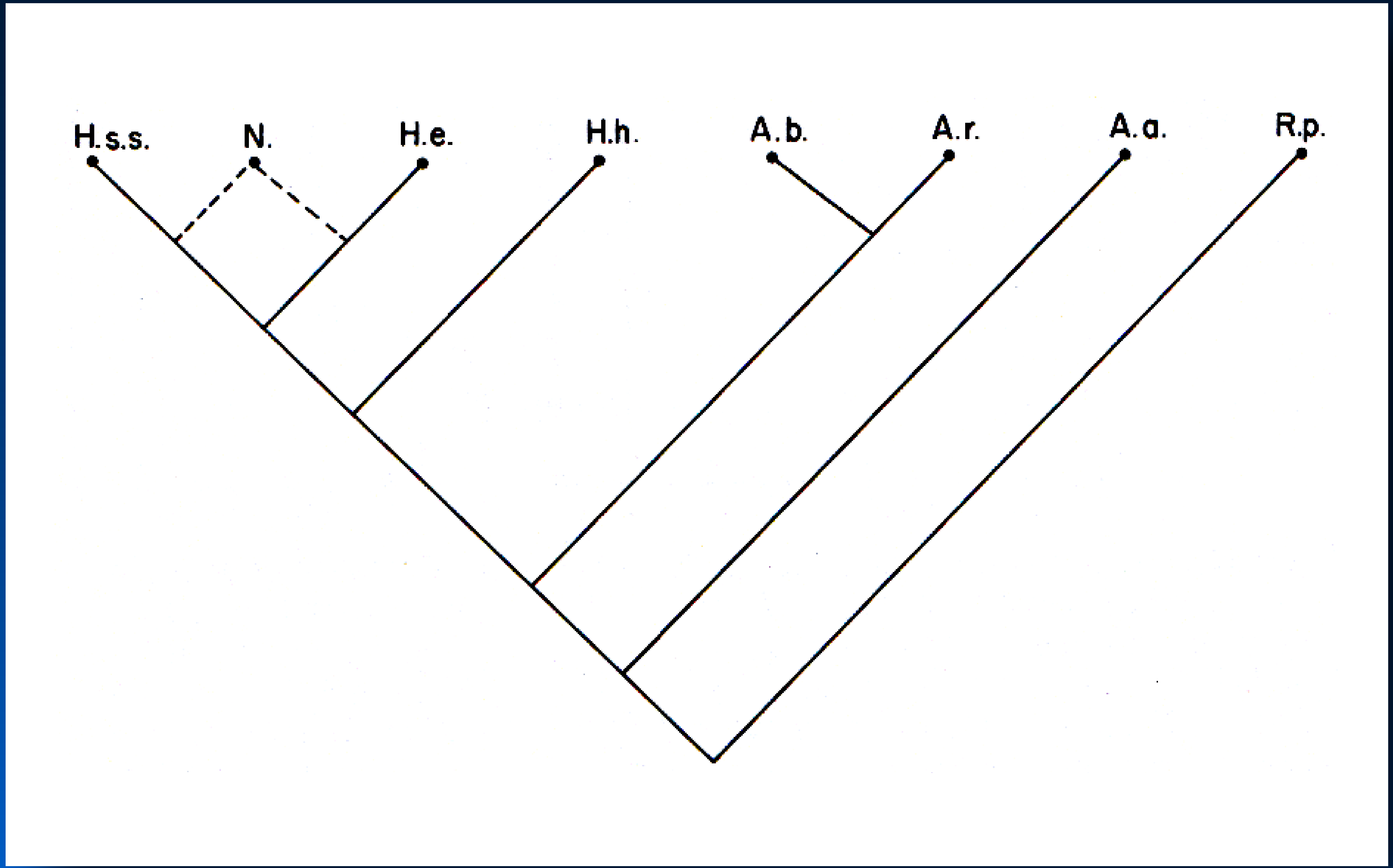
Turborotalia cerroazulensis

Turborotalia coccoaensis

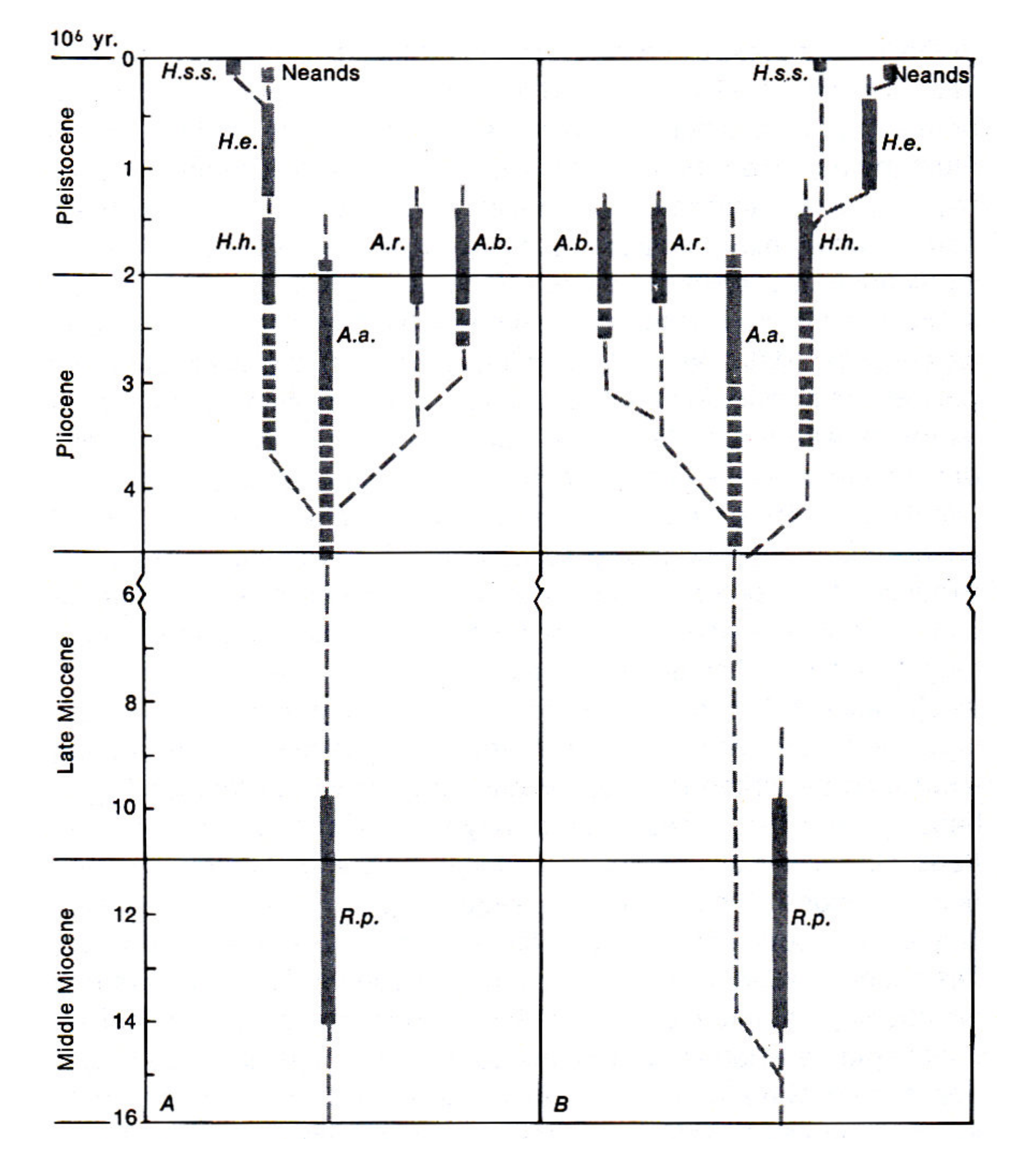
Turborotalia cunialensis

Phylogenetics, Cladistics & Phylogeny

Cladograms versus Phylogenetic Trees



Cladograms depict nested patterns of synapomorphies that reflect the pattern of phylogenetic relations between any set of taxa.



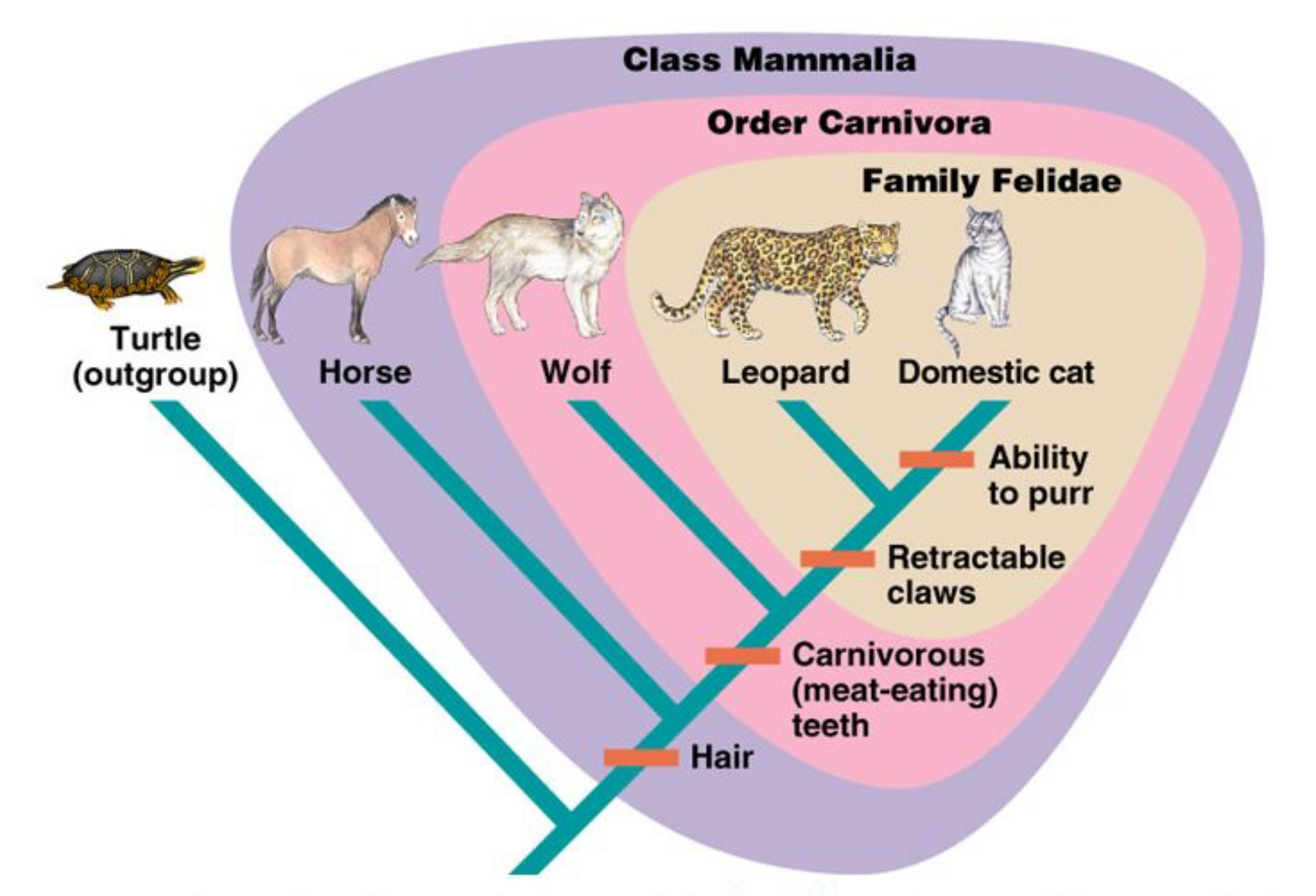
Phylogenetic trees specifies actual pattens of ancestry and descent between species over time.

Phylogenetics, Cladistics & Phylogeny

Phylogenetic Systematics

Advantages

- Focus on identification of synapomorphies allows monophyletic groups to be distinguished from paraphyletic and polyphyletic groups.
- Theory underpinning phylogenetic systematics quite stable, well-developed and widely accepted.
- Numerous algorithms and software applications are available for inferring and analyzing cladograms with more appearing on a regular basis.
- Currently the most widely practiced approach to phylogenetic inference.



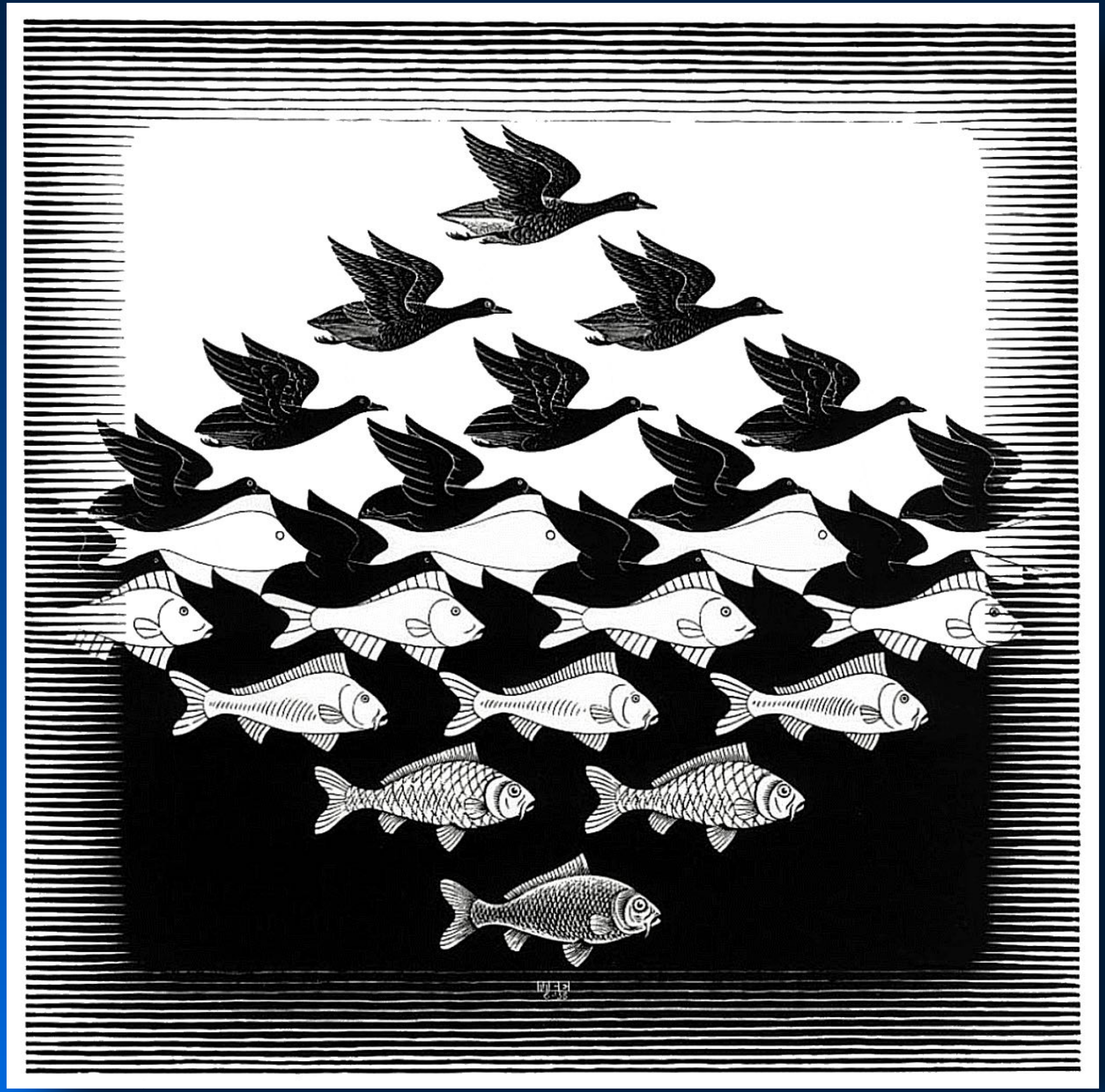
Disadvantages

- New advances in data-collection capability and data-analysis method render many cladistic phylogenies unstable and so unsuitable for serving as a basis for classification.

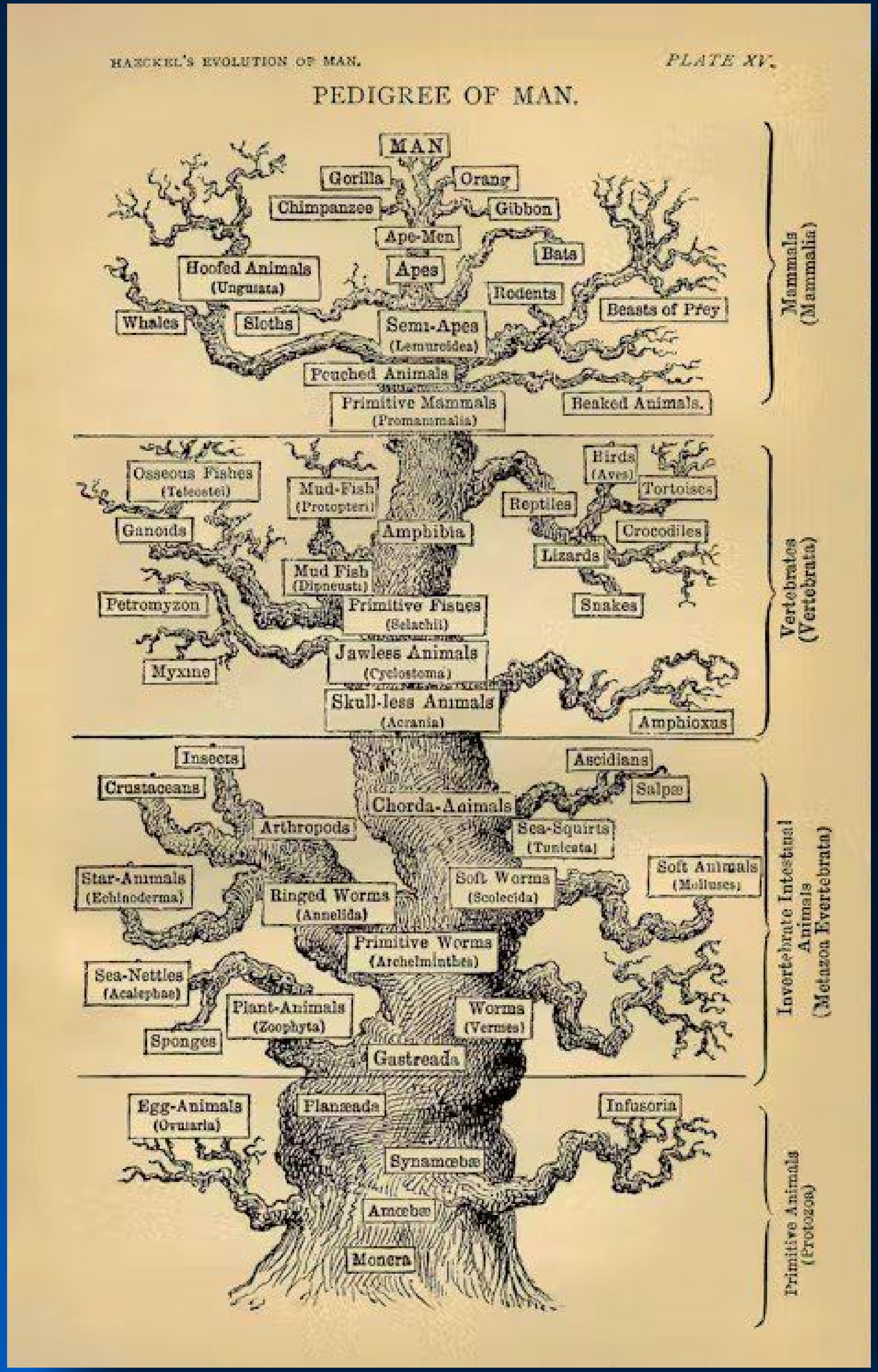
NJU Course

Principles of Paleobiology

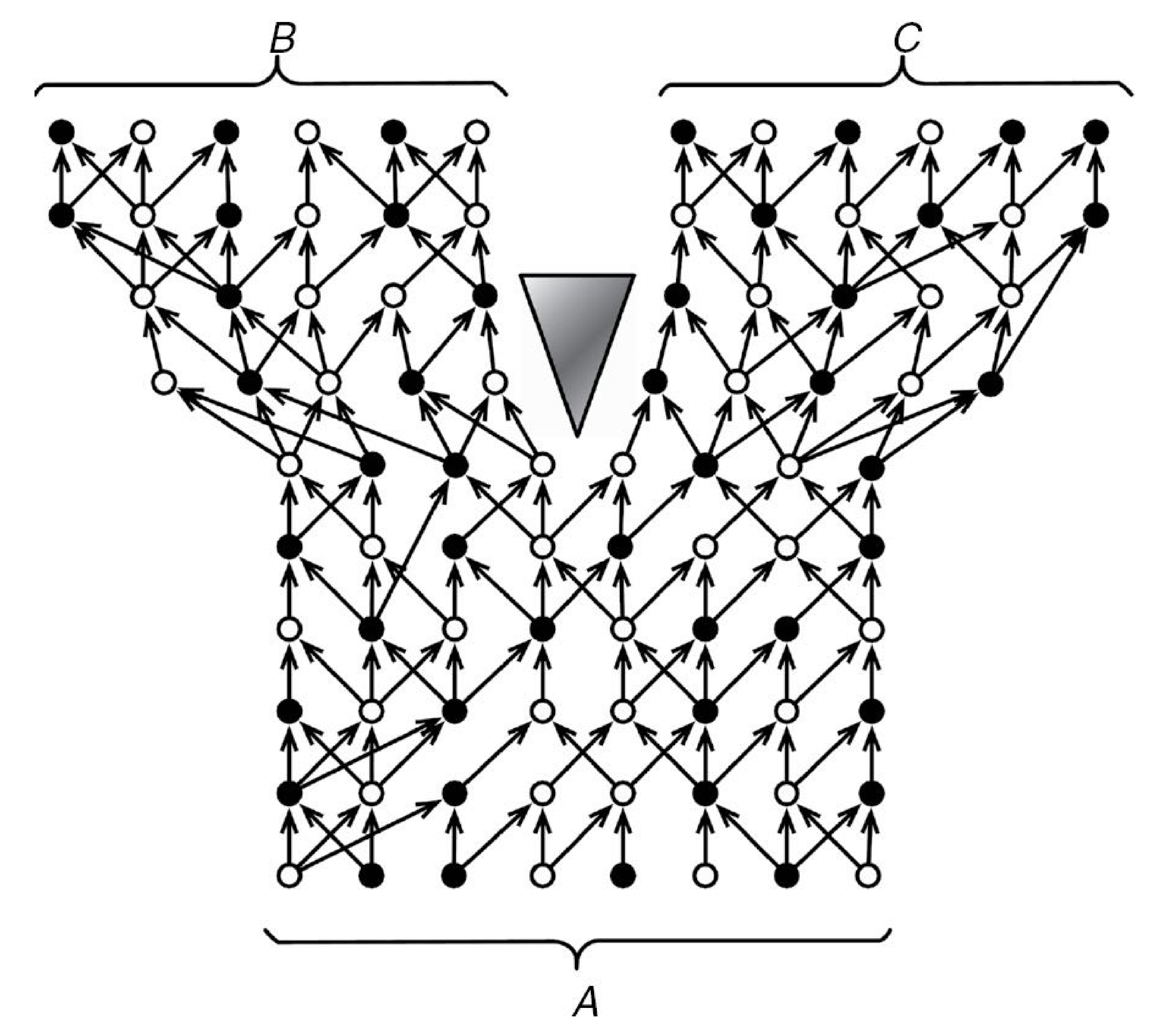
Phylogenetic Inference, Cladistics & Phylogeny



Sky and Water (M. C. Escher, 1938)



Haeckel (1866)



Hennig (1966)