Contributions of Linnaeus

Mainly the impact of *Systema Natura*. By the 10th edition it was an exhaustive list of species known to science with:

1. binominal nomenclature
2. telegram-style diagnoses
3. standardization of synonymies
4. classification by hierarchy

He also contributed many other systematic procedures (particularly in botanical systematics – terminology for plant morphology including standardization of sexual characters)

"Thus Linnaeus's 1738 polynomial for this species was
Veronica foliis oppositis, caule spica terminato, i.e., 6 words;
his 1745 polynomial
Veronica floribus spicatis, foliis oppositis, caule erecto, i.e., 7 words;
his 1753 polynomial
Veronica spica terminali, foliis oppositis crenatis obtusis, caule adscendente simplicissimo, i.e., 11 words.
The alternative two-word name
Veronica spicata,
introduced by Linnaeus in 1745 and retained by him in 1753, has remained unchanged to the present day. These two advantages were in fact noted by Linnaeus in his *Philosophia botanica* no. 257 (1751)" Stearn (1959)

Linnaeus' Higher Classification

recognized four categorical levels below kingdom:

1. class,
2. order,
3. genus,
4. species

Kingdom, Phylum, and Family added later.

Taxon - a group of related species worthy of ranking.
Category - a formal rank in the Linnean Hierarchy

Because he rejected evolution, he did not have compelling explanation for the cause of the hierarchical structure.

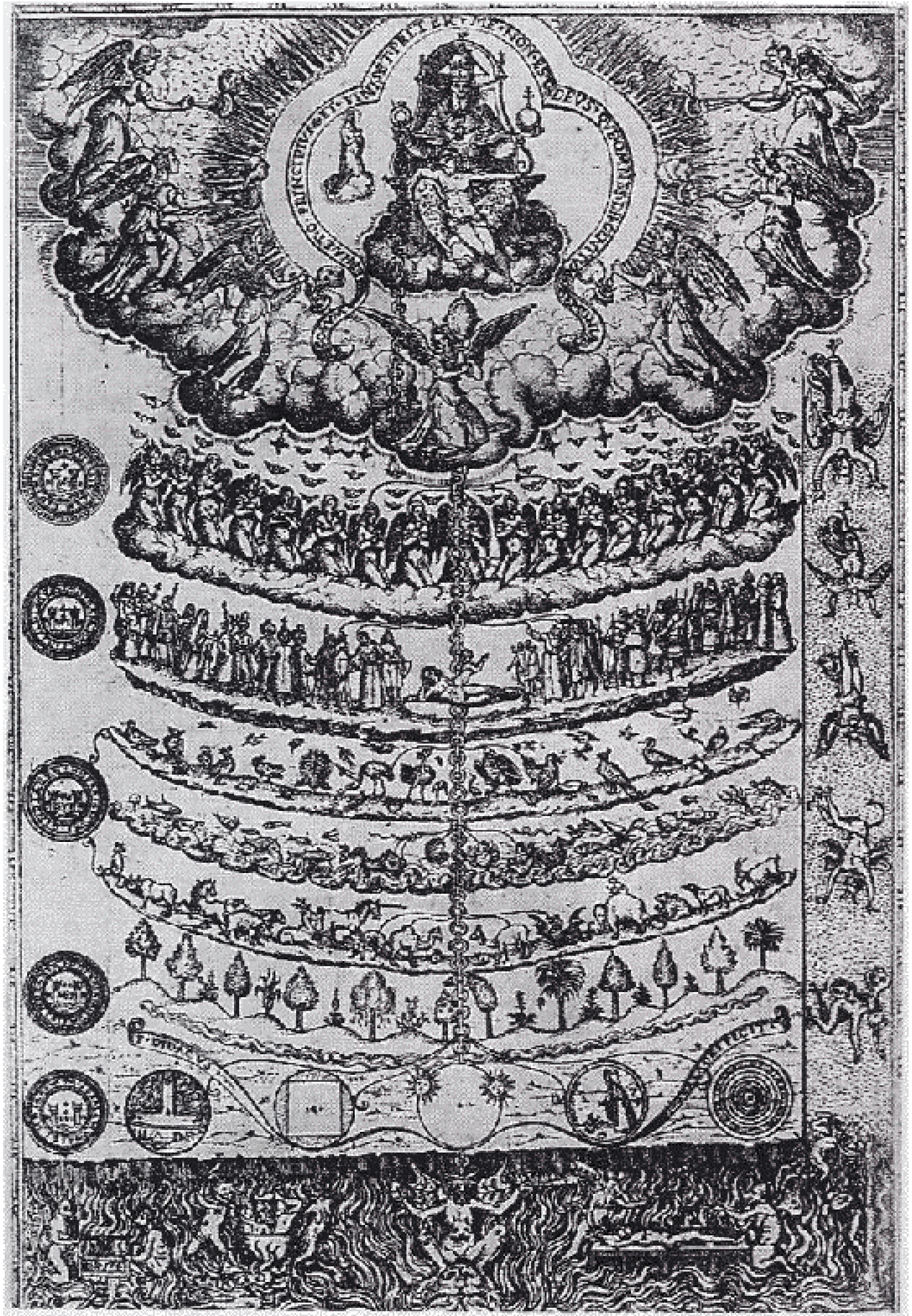
Crisis in theoretical systematics

What is the source of the similarities between organisms?

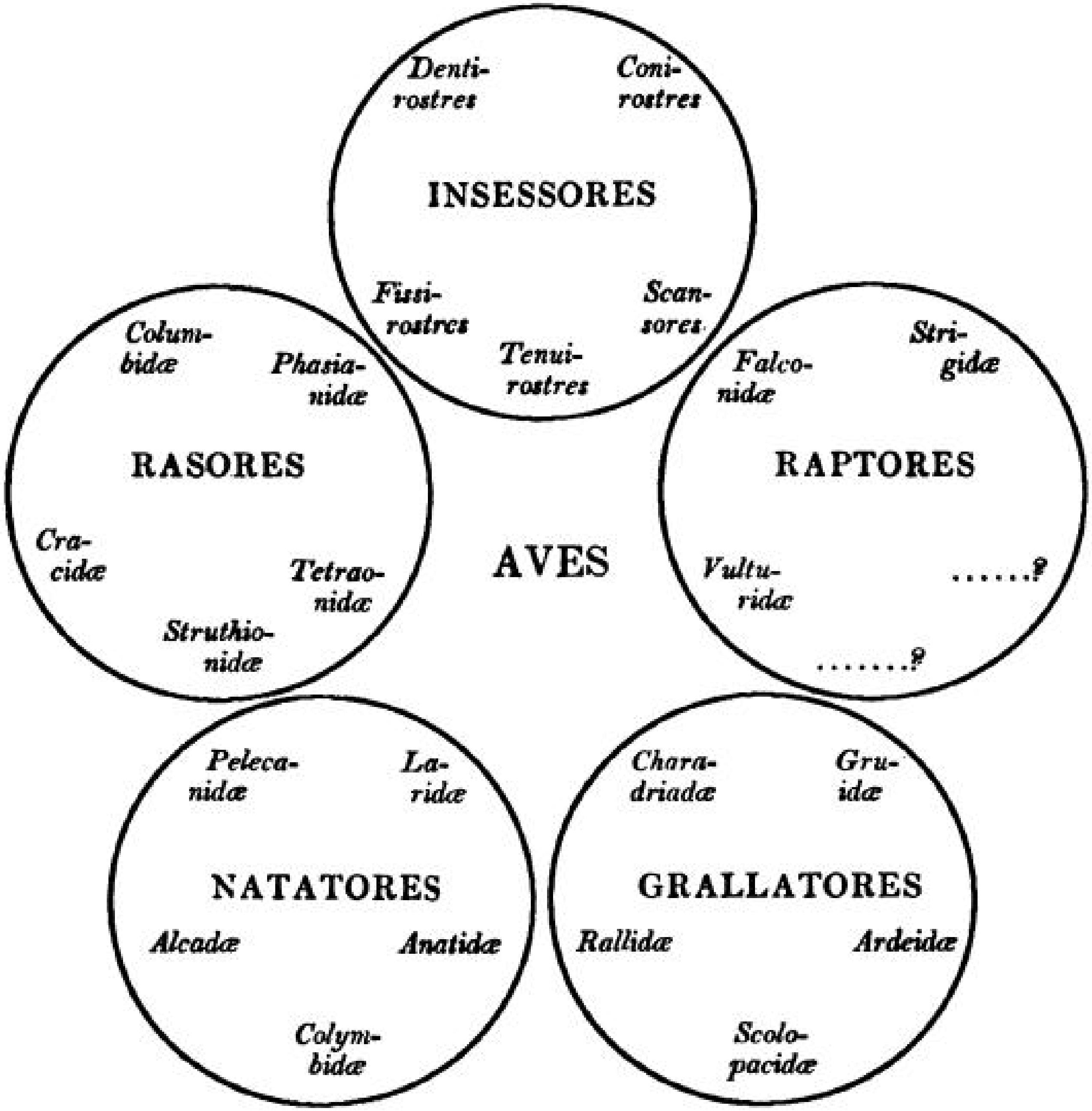
1. As the number of described species increased, *essential* characters (or sets of characters) were abandoned – move to similarity over finding *the essential* characters.
2. Evolution was supported by some (Saint-Hillaire and Lamark), but a compelling mechanism was lacking.
3. Buffon, Cuvier, and Agassiz were vigorous opponents of evolution – but they could not provide good explanations for the pattern to the diversity of life.

Scala Natura

1. Another unfortunate part of Aristotle's legacy to systematics (he believed in it, but probably did not invent it).
2. "naturalness" and "relatedness" reflected the thought patterns of God during the creation. Affinity was "direct result of those laws of organic life which the Creator enacted for his own guidance in the Act of Creation"(Strickland 1846 p356 quoted by Mayr and Ashlock, 1991).
3. The idea that natural diversity reflected a progression from most imperfect (inorganic molecular) to most perfect (man) on to angels and to God.
4. In biology, this became untenable fairly early (particulary in botany where we can't use similarity to humans).
5. Nevertheless, is deeply embedded in popular conceptions of natural diversity ("lower vertebrates").

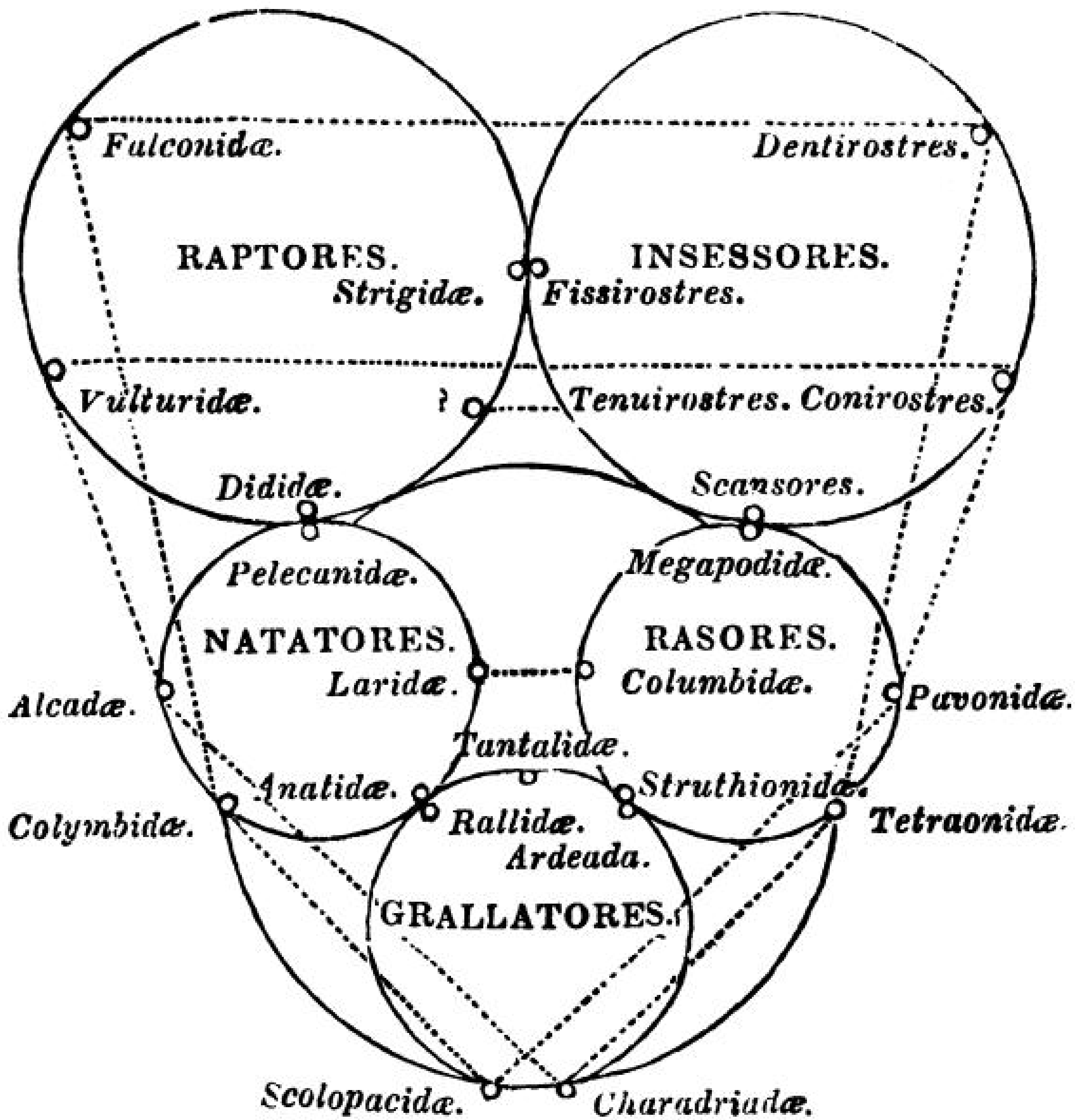


from http://upload.wikimedia.org/wikipedia/commons/b/b5/Great_Chain_of_Being_2.png



Quinarian arrangement of Vigors (1824). Question marks indicate taxa that were yet to be identified.

image from http://en.wikipedia.org/wiki/Quinarian



Affinities and analogies among the groups according to Swainson. The circles touch with groups on them having "affinities", but the lines connect groups that showed "analogies".

image from http://en.wikipedia.org/wiki/Quinarian

Analogies of the Five Orders of the Ptilota.

Orders of the *Ptilota.*	*Analogies.*	Classes of the *Vertebrata.*
LEPIDOPTERA.	Wings highly developed.	BIRDS.
HEMIPTERA.	Wings imperfect, or none.	QUADRUPEDS.
HYMENOPTERA.	Tail often armed with a sting.	REPTILES.
COLEOPTERA.	Most imperfect of their respective circles.	AMPHIBIANS.
NEUROPTERA.	Pre-eminently aquatic.	FISHES.

from William Swainson's 1840 book:

"On the history and natural arrangement of insects"

image from http://en.wikipedia.org/wiki/Quinarian

The impact of the recognizing evolution on systematics

1. Genealogical relationships between species could serve as the basis for taxonomy
2. Two sources of similarity:
   (a) similarity from descent
   (b) similarity caused by convergence (driven by natural selection for the same function).

Phylogeny as the basis of Taxonomy

Before the acceptance of evolutionary theory, “related” and “naturalness” where used with a variety of meanings.
After Darwin “genealogically related” when we say “related” and we could *define* “naturalness” of taxa by whether or not they recognize clades.

clade – a branch of a phylogenetic tree including an ancestral species and *all* of its descendants.
monophyletic – the adjective form (from the Greek words “mono” for one and “phylon” for race, class or tribe). A clade is a monophyletic group.

Darwin's largest contributions to systematics

1. provided a theoretical base for understanding the existence of the Linnean hierarchy and "relatedness" among organisms.
2. provided the expectation for a historical continuity among organisms – led to an emphasis on phylogeny reconstruction that underpins current systematics.

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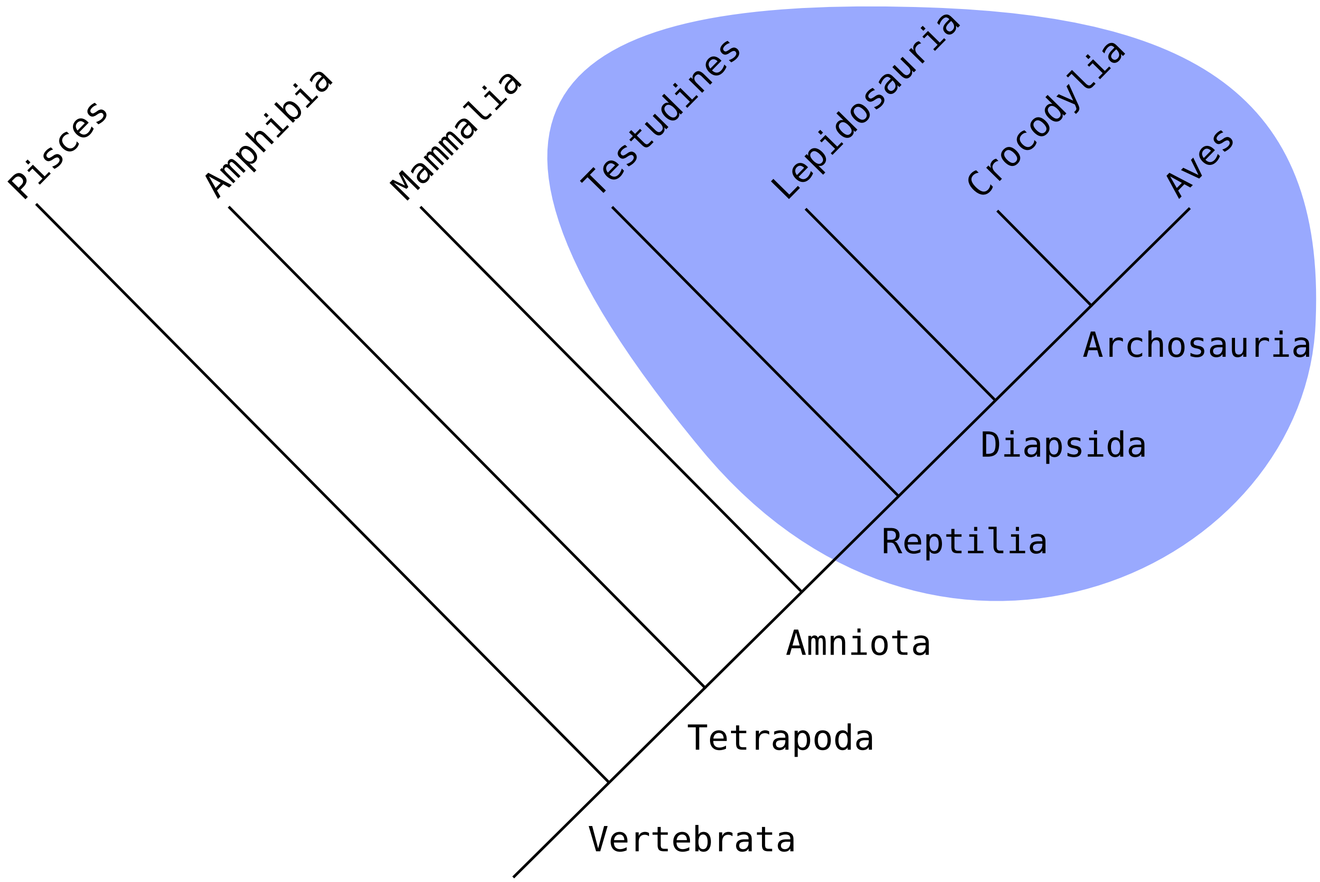

Monophyly

image from http://en.wikipedia.org/wiki/Monophyly

The impact of the recognizing evolution on systematics

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Similarities from common descent – “homologous characters”

- may exhibit anatomical correspondences coupled with functional difference – co-opting of existing structures.
- similarity in seemingly arbitrary features – “frozen accidents”

Convergent (“analogous”) characters tend to:

- have similar function, and similar in form on a gross level – differ in details.
- present problems when we try to imagine a continuum of descent (final structure made by different parts, or significant devolopmental differences).
- have obvious fitness implications.

These “rules of thumb” too vague to provide an error-proof means of distinguishing from homology, but they capture a key insight of evolutionary thinking.

Taxonomy after Darwin

A burst of interest in phylogeny reconstruction, e.g., tree like constructions of Haeckel(1860 - 1890's).

But in the late 1800's and early 1900's there was a decline in systematics:

1. uncertainty about the reliability of phylogeny reconstruction and how to separate this from classification (conceptual problems)
2. disappointment in failure to resolve higher level phylogeny.
3. practical procedure for inferring phylogenies were lacking –
4. growing competition from other emerging branches of biology (embryology, cytology, Mendelian genetics, physiology, biochemistry, etc.)

5. Development of the codes of nomenclature became a focus of some researchers
6. Rise of population thinking became a focus of systematists. With the growth of the field of genetics and an understanding of the structure of populations, a new direction was forged for systematics.

International codes of nomenclature

Zoology (1901)
Botany (1930)
Bacteriology (1947)
The codes provided for:

1. rules for choosing among competing names
2. rules for how names must be proposed to be valid.

“The New Systematics”

book of that title by Huxley, J. (1940) gave its name to the movement – blended into the Modern Synthesis of evolutionary biology.

- a merger of “evolutionary taxonomy”, genetics, and theory of populations
- Concentrated on ‘microtaxonomy’ – species, subspecies and populations.

Phylogenetics before the 1960's

1. Many systematists conceded that phylogeny should be the basis of taxonomy but were very pessimistic about the prospects of inferring phylogenies.
2. Phylogeny estimates were the results of *ad hoc*, inscrutable analyses by experts rather than clear protocols.
3. There was debate on whether or not phylogenetic information should be the *only* information affecting taxonomy.

Three schools of Systematics

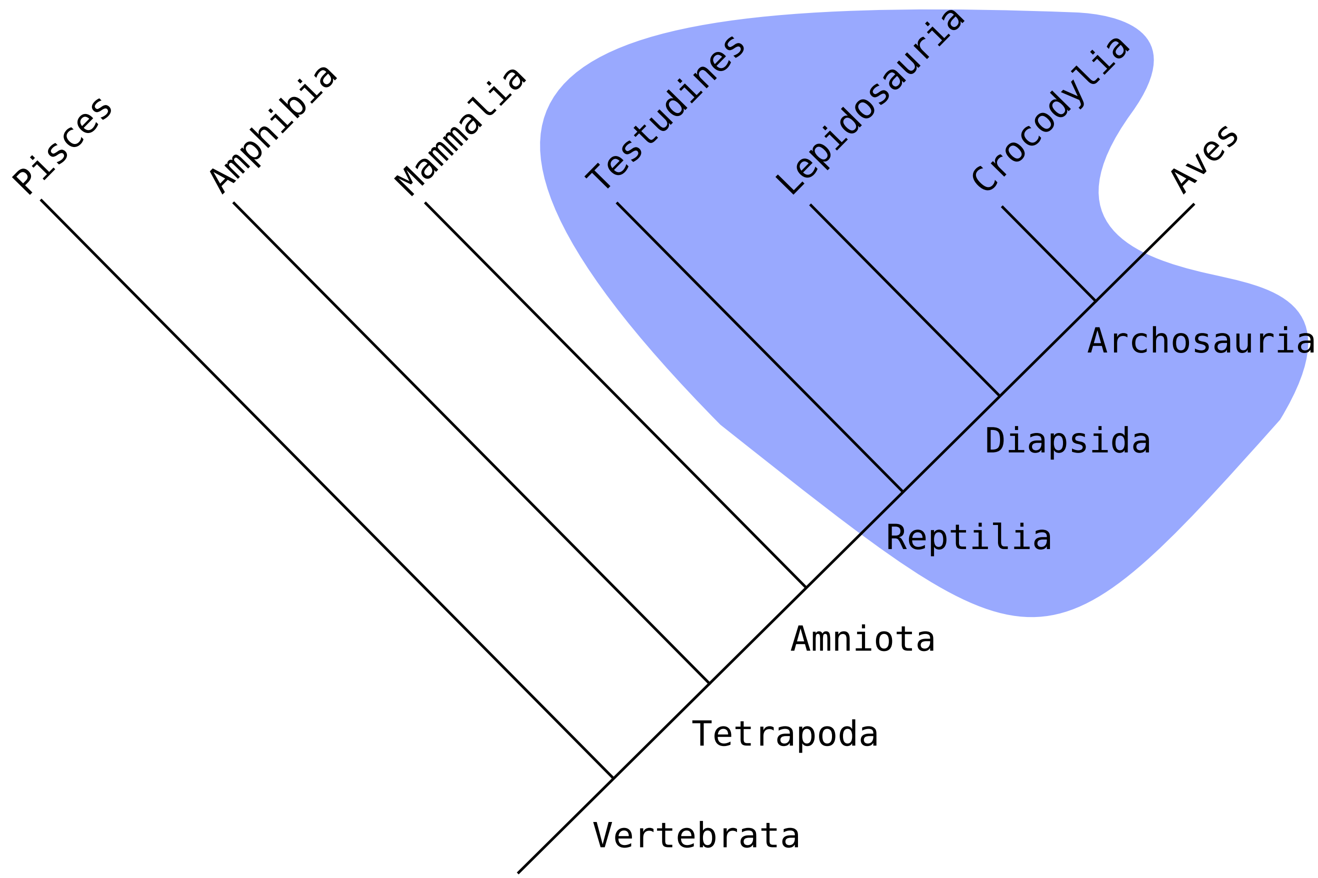
	Evolutionary Systematics	Phenetics	Phylogenetic Systematics
We can estimate phyologenies for most groups?	?	No	Yes
Taxonomic procedures must be standardized?	?	**Yes**	Yes
Taxonomy should reflect phylogeny only?	No	No	Yes

Evolutionary Systematics

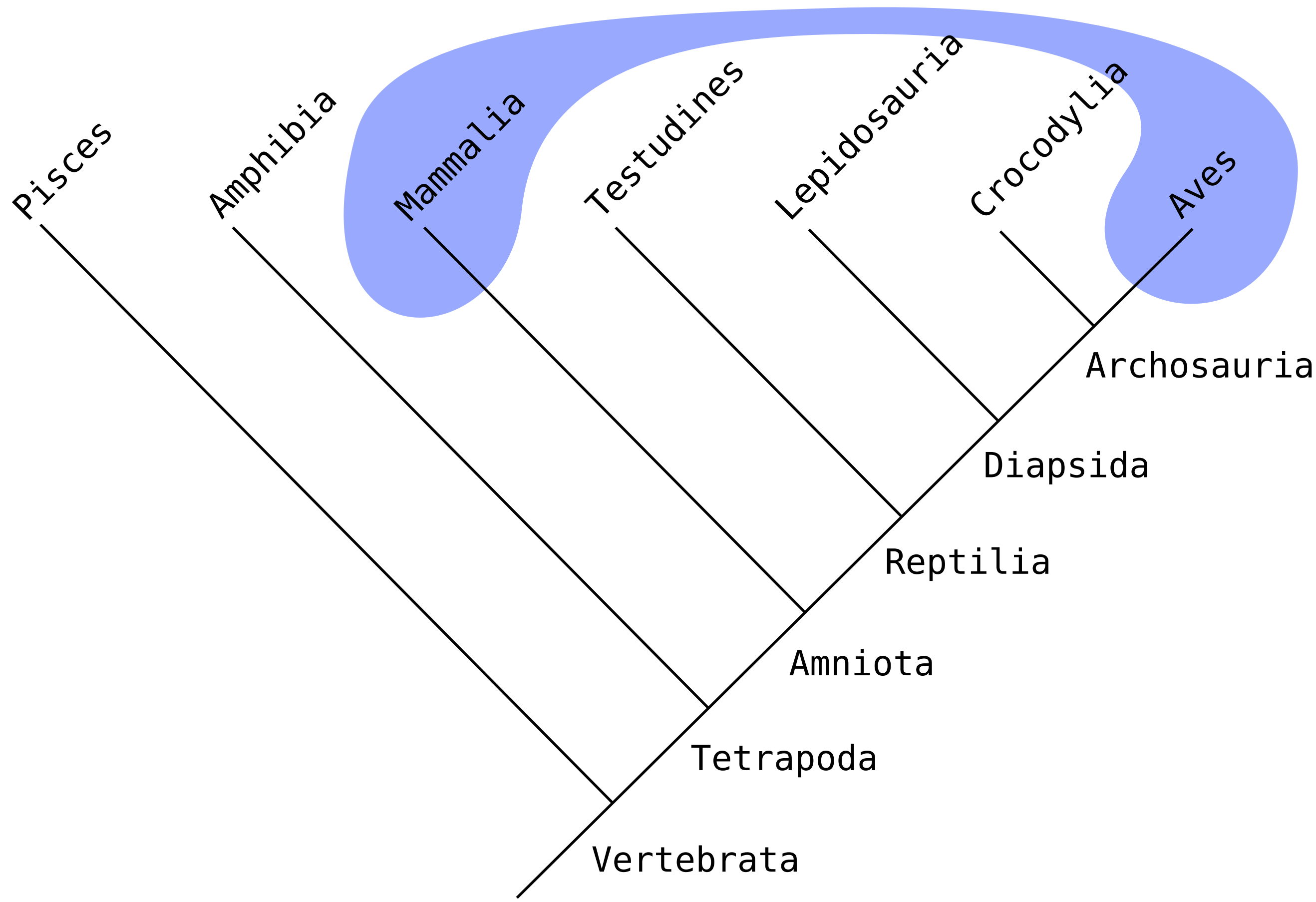
Different types of evolutionary change

1. **cladogenesis** - speciation, splitting of a lineage into 2 or more descendants
2. **anagenesis** - change within a lineage.

"Evolutionary" systematists felt that *both* types of changes must be reflected in classification – so that classification reflected both major components of evolution.



Paraphyly
image from http://en.wikipedia.org/wiki/Monophyly



Polyphyletic
image from http://en.wikipedia.org/wiki/Monophyly

Criteria for Delimitation and Ranking of a group

Quoted (or paraphrased) from page 267 Mayr and Ashlock (1991)

1. Distinctness (size of gap between groups)
2. Degree of difference (within a group - tight clusters argue for ranking).
3. Evolutionary role (uniqueness of adaptive zone)
4. Grade characteristics. grades are – “similar in general level of organization” (Simpson, 1961). E.g. prokaryotes.
5. Size of taxon
6. Equivalence of ranking in related taxa (balance)
7. Stability

Classic examples of the evolutionary systematics approach

1. Aves and Reptilia as classes – despite the fact that some "Reptiles" (e.g. crocodylomporhs) are more closely related to birds than they are to lizards.
2. Huxley (1940) suggested that humans should be in their own phylum – "Psychozoa" – because reasoning and rational thought were particularly important innovations.

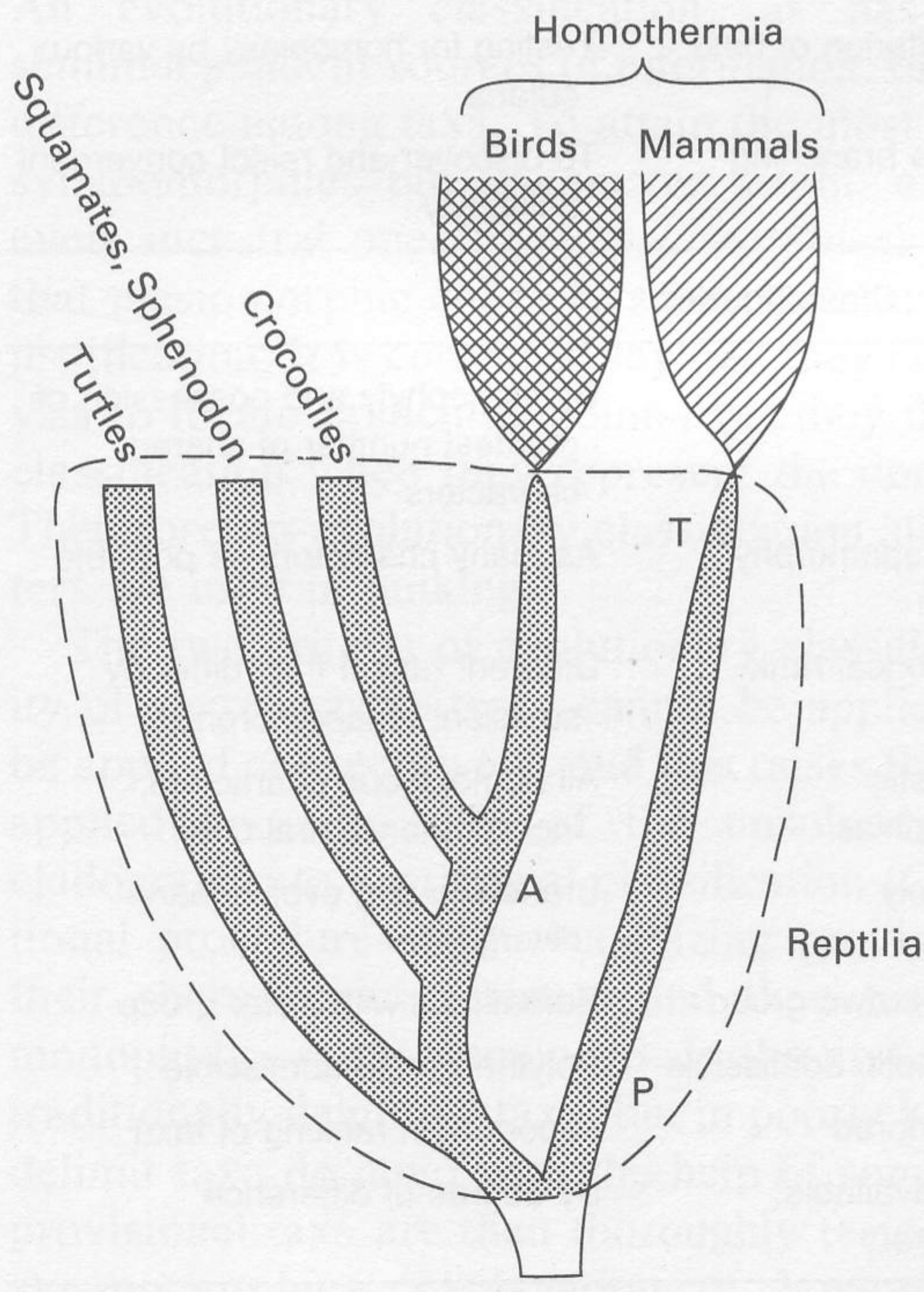


FIGURE 10-3
A phylogeny of the Recent classes of Amniota, with the monophyletic (though paraphyletic) Reptilia, the two holophyletic ex-groups Birds and Mammals, and the invalid convergently polyphyletic taxon Homothermia. A = Archosauria, P = Pelycosauria, T = Therapsida. (*After Carroll 1988.*)

From Mayr and Ashlock, 1991

Numerical taxonomy – phenetics

1. choose the specimens OTU's: operational taxonomic units
2. choose and measure characters (largest number possible).
3. treat characters equally
4. code the characters in a matrix
5. produces a similarity matrix.
6. use clustering methods to group OTU's

The abandonment of numerical taxonomy

1. weighing all characters equally does not exploit our knowledge of evolution.
2. Objectivity of analyses undercut by subjectivity in selecting characters. Lack of unifying theory made it hard to justify one coding over another.
3. Loss of information from summarizing characters together as a similarity matrix.
4. Failure to distinguish between analogy and homology (gives up one of the biggest advantages of taking a systematic approach).

Positive: much needed emphasis on explicit procedures in data collection and analysis.

Phylogenetic systematics – “cladistics”

1. Phylogenetic classification system would be the most useful as a general reference system for all of biology
2. Phylogenetic relationships could be uncovered by analysis of characters.
3. Shared, derived characters were useful in uncovering relationships. Shared, primitive characters were **not**.
4. Relative recency of common ancestry is the only aspect of phylogeny to be captured in classification – **not** degree of divergence.

When a cladist says "species A and species B are members of the same monophyletic group but species C is not" then we know the phylogeny:
((A,B),C)

When an evolutionary systematists makes the same statement, we do not know the tree. We don't know which of the 7 reasons for grouping he/she is applying when A+B are recognized as a group.

By trying to put too much in a classification (cladogenesis and anagenesis), the evolutionary systematists made their classifications too difficult to interpret.

Three schools of Systematics

	Evolutionary Systematics	Phenetics	Phylogenetic Systematics
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Taxonomic procedures must be standardized?	?	**Yes**	Yes
Taxonomy should reflect phylogeny only?	No	No	Yes

Other major developmens in modern systematics

1. The molecular biology revolution dramatically expanded our source of characters.
2. Phylogenetic inference as a problem in statistical inference.
   (a) better assessments about how confident we should be in different aspects of phylogenetic inference,
   (b) better integration with other parts of biology (to infer trees more reliably and to use trees to answer evolutionary questions).
   (c) phylogenetic estimates are more robust to potential confounding “noise”,
   (d) more powerful estimators, and
3. Phylomath

References

Mayr, E. and Ashlock, P. D. (1991). *Principles of Systematics Zoology*. McGraw-Hill, New York, 2nd edition.

Stearn, W. T. (1959). The background of linnaeus's contributions to the nomenclature and methods of systematic biology. *Systematic Zoology*, 8(1):4–22.