Introduction to Biosystematics - Zool 575

Introduction to Biosystematics
Lecture 10 - Introduction to Phylogenetics

1. Pre Lamarck, Pre Darwin
   “Classification without phylogeny”

2. Lamarck & Darwin to Hennig (et al.)
   “Classification with phylogeny but without a reproducible method”

3. Hennig (et al.) to today
   “Classification with phylogeny & a reproducible method”

Outline - History and introduction to phylogenetic inference

1. Pre Lamarck, Pre Darwin
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History

Aristotle - Scala Naturae - ladder of perfection with humans at top - DIFFICULT mental concept to dislodge! (use of terms like “higher” and “lower” for organisms persist)

Linnaeus - perpetuated the ladder-like view of life linear, pre evolution

1758 - Linnaeus grouped all animals into 6 higher taxa:
1. Mammals (top)
2. Birds
3. Reptiles
4. Fishes
5. Insects
6. Worms (bottom)

History

Lamarck - 1800 - Major impact on Biology:
- First public account of evolution - proposed that modern species had descended from common ancestors over immense periods of time - Radical evolution = descent with modification
- Began with a ladder-like description... but considered Linnaeus’s “worms” to be a chaotic “wastebucket” taxon
- He raided the worm group to liberate disparate taxa
- Early and MAJOR example of using data interpreted within an evolutionary framework to classify

History

- Phylogenetics began before “evolutionary trees”
- Classifications were taken as proxies - representations of the “natural order,” these were the “trees”
- By putting taxa together in a group, one was saying “these taxa are closer to one another than to anything else - they belong together”
- “Closer” meant different things to different workers:
  e.g. Greater body form similarity / complexity
  e.g. Greater evolutionary relationship
  e.g. more shared homologies...
  (natural vs artificial)

Perhaps the first branching diagram, “phylogentic tree” published in the history of Biology - 1809

Lamarck’s ideas:
- Two origins of life (since both were “equally primitive”) Insects et al - side branch
- Removed birds to side branch rather than “below” mammals

Lamarck, J. B. 1809. Philosophie Zoologique
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**History**

"Dans sa production des differents animaux, la nature n'a pas execute une serie unique et simple."

(In its production of the different animals, nature has not fashioned a single and simple series.)

- Lamarck 1815

= the beginning of the end of the Scala Naturae

**History**

Charles Darwin (& Alfred Russel Wallace) - provided the mechanism (natural selection) to explain evolution - 1858 & 1859

Lamarck's ideas, which lacked an accurate mechanism, hadn't spread

Darwin's ideas did...

(That evolution occurred was apparent to many who knew the fossil record, the problem, was "How?")

**History**

"In regard to classification and all the endless disputes about the "Natural System," which no two authors define in the same way, I believe it ought, in accordance to my heterodox notions, to be simply genealogical.

But as we have no written pedigrees you will, perhaps, say this will not help much; but I think it ultimately will, whenever heterodoxy becomes orthodoxy, for it will clear away an immense amount of rubbish about the value of characters, and will make the difference between analogy and homology clear. The time will come, I believe, though I shall not live to see it, when we shall have very fairly true genealogical trees of each great kingdom of Nature."

Darwin in a letter to Huxley, 1857

**History**

Classifications (starting in the mid to late 1800s)

- Based on inferred evolutionary history
- End of artificial classifications for convenience or for understanding the creator
- But, "How does one infer evolutionary history?" no reproducible method, yet, to do so...

**History**

Ernst Haeckel (late 1800s)
- Heavy supporter of evolution, but not Darwin
- "Ontogeny recapitulates phylogeny" - not a law, as he thought
- Coined terms:
  - Ecology
  - Phylum
  - Phylogeny

**History**

The "method" of phylogenetic inference (from which one may or may not derive a classification) that developed is referred to as

Evolutionary Taxonomy
- spanned from the 1800s to the 1960s
- formed the “roots” of the discipline of phylogenetics
History

Evolutionary Taxonomy (<1960s)
- "Method" involved a reliance on authority, not reproducible:
  1. Spend a lifetime learning as much as possible about the biology of a group (morphology, development, fossils, etc.)
  2. Publish a drawing of a phylogeny based on one’s (informed) opinion = “Guessograms”

Evolutionary Taxonomy (<1960s)
- During the modern synthesis systematics was marginalized “not a science”
- Leading figures: Mayr & Simpson 1940s
- Without a reproducible method, hypotheses couldn’t be tested
- No longer used, but exists in some forms today (in contrast to systematists who know nothing about their organisms!)

Summary of contributions

Evolutionary Taxonomy (<1960s)

Good: "Know your organisms"
Bad: not reproducible; no objective method; arbitrary, intuitive, no way to resolve conflicts

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Lack of a reproducible method resulted in three major approaches: (Explosion in 1960s)

1. Phenetics - similarity / distances only, not evolution, not phylogeny
2. Cladistics - phylogeny inferred using characters & parsimony
History
Phenetics - similarity only, not evolution, not phylogeny (1950-1960)
- computerized, reproducible, “objective,”
  modern, sexy...
- goal to remove all subjectivity, measure everythin
  g, use matrix of distances
- cluster based on overall similarity
- not evolutionary trees, but phenograms

Phenetics - Problems
1. Reproducible but no agreement on which clustering algorithm or statistic to use...
   - different algorithms = different trees
     e.g. UPGMA, PCA... etc.
   - although there is only one true evolutionary tree, there are many alternative
     ‘similarity’ trees depending on the data & algorithm used
2. Similarity doesn’t always = evolutionary relationship!

History
Phenetics - the good
1. Demanded explicit character analysis & laid groundwork for numerical phylogenetics
2. Still used for lower-level problems
   e.g. morphometrics, species demarcations...
3. And some higher-level problems
Survives in various forms - an issue of debate...
(see lecture on Distance methods)

Lack of a reproducible method resulted in three major approaches:
1. **Phenetics** - similarity / distances only, not evolution, not phylogeny
2. **Cladistics** - phylogeny inferred using characters & parsimony
3. **Statistical Phylogenetics** - phylogeny inferred using characters & “best fitting model”
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**History**

**Cladistics**
1950 - Willi Hennig "Grundzüge einer Theorie der phylogenetischen Systematik"
- German entomologist of Diptera
- 1966 English translation of Phylogenetic Systematics
- key: distinguish derived from ancestral homology
- yields phylogenetic tree
- Vitiolic attacks on phenetics during the 1970s

**History**

**Cladistics**
- method explicit, reproducible
- hypotheses of phylogeny could now be "tested"
- Hennig’s original method:
  1. Distinguish homologies from analogies
  2. Distinguish derived homologies (apomorphies) from ancestral (pleiomorphies) homologies
  3. Tree then built from apomorphies (evidence of common ancestry)
- more on how this is done later

**History**

**Cladistics - monophyletic classification**
- a new method for phylogenetic inference AND
- a new method to derive classifications
  1. Not based on similarity but on phylogeny (attacked phenetic clusterers)
  2. Taxa must be natural (monophyletic)
     = common ancestor and ALL descendents included
     (attacked ET classifications that accepted non-monophyletic groups)

**Classifications and Phylogenies**

Given this classification:
- Class Reptilia
  - Order Anapsida (turtles)
  - Order Lepidosauria (lizards & snakes)
  - Order Crocodilia
  - Class Aves
  - Class Mammalia

What evolutionary tree would you envision?

**History**

**Cladistics**
- Originally lacked an explicit method to deal with character conflict: “Hennig’s dilemma”
- Hennig’s approach was to remove the conflict by restudy of the characters
- The principle of Parsimony was later employed to deal with character conflict (to be continued…)

**Reptilia is not monophyletic**
It is a grade, not a clade

Does not include 2 descendent groups: mammals & birds
Lack of a reproducible method resulted in three major approaches:

1. **Phenetics** - similarity / distances only, not evolution, not phylogeny
2. **Cladistics** - phylogeny inferred using characters & parsimony
3. **Statistical Phylogenetics** - phylogeny inferred using characters & "best fitting model"

### Statistical Phylogenetics
- Grew from mathematical, computer, evolutionary, numerical studies, not as much from systematics
- Concurrent with first protein sequence data (Zuckerkandl & Pauling, 1962)
- 1960s numerical techniques that used characters rather than distances/similarities:
  1. **Parsimony** (Cavalli-Sforza & Edwards, 1963)
     - tree with minimum changes preferred
  2. **Maximum Likelihood** (Cavalli-Sforza & Edwards, 1964)
     - tree that maximizes probability of the data is preferred

### History
#### Statistical Phylogenetics
- Cavalli-Sforza & Edwards had been students of the population geneticist R. A. Fisher
- Worked on trees of human populations from gene frequencies & blood group alleles
- Arrived at 2 methods initially:
  1. Parsimony
  2. Least-squares (a distance method)
- 3rd method to reconcile the two:
  3. **Maximum Likelihood** (Fisher's method)
     - published 1964 & 1967

#### Statistical Phylogenetics & Cladistics
- Cladists state that Hennig's methods "implied" parsimony:
  - Hennig's **Auxiliary Principle**: assume homology if there is no evidence to the contrary
    - one change (homology) is the default assumption over
    - two or more changes (analog/ homoplasy)
    - prefer trees with the greatest number of apomorphies (and thus the fewest homoplasies)

- Camin & Sokal's parsimony required irreversible change & ordered states (problem)
  \[ 0 \Rightarrow 1 \Rightarrow 2 \Rightarrow 3 \]
- Parsimony becomes adopted by the cladists:
- Kluge (1969) and Farris (1970) published algorithms for unordered parsimony termed "Wagner Parsimony" & how to search for the most parsimonious tree

- evolved cartoon "Caminalcles" & tested methods to infer the "known" phylogeny
- parsimony was best
**History**

**Statistical Phylogenetics & Cladistics**
- Cladists (most) reject statistical approaches to phylogenetics
- In so doing they consider parsimony to not be statistical but philosophical
- Claim justification for a “parsimony-only” method using arguments on hypothesis testing of philosopher Karl Popper
  (more on this later…)

**History**

**Statistical Phylogenetics**
- Initially overshadowed by cladistics difficulties with complexity of approach
- Rapidly expanding field initially for molecular data now (2001) for morphological faster algorithms & computers making approach fully practical
- Cladists continue the battle for their method

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**Terms** - from lecture & readings

- Aristotle's Scala naturae
- Lamarck
- Darwin
- Wallace
- Haeckel
- Evolutionary Taxonomy
- Mayr & Simpson 1940s
- phenetics
- Sokal & Sneath
- cladistics
- statistical phylogenetics
- Hennig
- Grade
- clade
- apomorphy
- plesiomorphy
- monophyletic classification
- parsimony
- maximum likelihood
- Cavalli-Sforza
- Edwards
- Camin
- Kluge
- Farris
- Hennig's Auxiliary Principle

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**You should be able to**

Describe the 3 phases in the history of phylogenetic inference

When did Phylogenetic Inference begin (approximately) & by whom?

Describe “method” of Evolutionary Taxonomy

Describe explosion of methods in 1960s

Describe the pros & cons to each method

Who was key to each method?

Why isn’t a phenogram a phylogeny?