

Lecture 2 – The History of Phylogenetic Inference

I. Introduction. Inference of evolutionary history has been of interests since descent with modification was established over 160 years ago. It's a discipline with a varied and checkered history and has been deeply embroiled in often-venomous debate.

Haeckel's evolutionary trees are famous and among the first attempts at phylogeny inference.

For the first century of evolutionary biology, there really was no objective methodology to how biologists would derive such evolutionary trees.

Numerous explicit approaches have been proposed and there has been very acrimonious debate as to the relative merits of each of these. This continues, but to a much lesser degree than has been true in the past.

I think it's important to have some familiarity with the history of this debate (science is not a Markov chain). Joe provides a unique historical perspective in Chapter 10, which is an important read. However, he has done a remarkable job in deleting much of the acrimony (often personal) that has characterized this history of phylogenetics.

The historical debates about phylogeny inference are, to some degree, grounded in debates about classification.

II. These alternative approaches have been placed into three classic **schools of thought**.

A. Evolutionary Taxonomy – This traditional school was predominant until the 1960's. This is essentially the Haeckelian school and relies on *expert opinion*. Felsenstein has omitted discussion of this approach from his book, but I think we should acknowledge the school, because of its long history and its status as the origin of the discipline.

The basic view was that the best way to reconstruct the phylogeny of a group is to spend a lifetime learning everything one can about the biology of the group.

The specialist (who then became the authority) then published a phylogeny based on his or her views.

Many were paleontologists and were happy to assign formal recognition to paraphyletic groups. Examples include, Cynodontia (in its classical formation), the group from which mammals evolved, and the classic paraphyletic group Reptilia.

Exemplified by Darwin's famous sketch (especially the "I think" part).

This had the advantage of generating incredibly well knowledgeable experts in the biology of particular groups (e.g., ecology, physiology, and repro. biol., behavior, etc.).

However, there was no objective methodology, and the results were therefore not reproducible.

The effect that this school had on the perception of systematics was quite dramatic. As the modern synthesis proceeded, systematics was marginalized to a “service discipline” that was thought to have no important contributions to make to evolutionary biology.

However, it should be pointed out that many of the relationships that the ET’s posited have been supported by application of modern phylogenetic methods. So, the phylogenies produced by at least some practitioners of ET were actually pretty good estimates, although there was no way to tell at the time.

B. Phenetics - In the late 1950's early 1960's, a group of biologists attacked Evolutionary Taxonomy as non-scientific based on its lack of an objective methodology. This introduced the tradition of contentious debate that only recently has waned.

The view of pheneticists (particularly **Sokal, & Rohlf**) was that **there is no way to infer the pattern of common ancestry of a group in a scientific manner**. Therefore, they argued, **we should group, or classify, organisms on the basis of overall similarity**.

As many measurements were taken as possible, and a variety of clustering methods were developed to arrange taxa in a similarity hierarchy. This is the origin of Numerical Taxonomy

Methods included UPGMA and many kinds of clustering procedures, like Principal Components Analysis, Canonical Variate Analysis, etc. Phenetics really has advanced the science of clustering, which is extremely important outside systematics.

Since the view was that phylogeny can't be inferred reliably, the goal was to produce a phenogram. This was not meant to depict evolutionary relationships, but to visualize a hierarchical pattern of overall similarity.

C. Cladistics - The level of vitriol in the debate was increased by the cladists. Its adherents often use the term **Phylogenetic Systematics**, and this is meant to imply that other approaches are not phylogenetic.

In the late 1960's, the work of the German entomologist Willi Hennig was published in English. Hennig is credited with founding the school of Cladistics, although others were important as well.

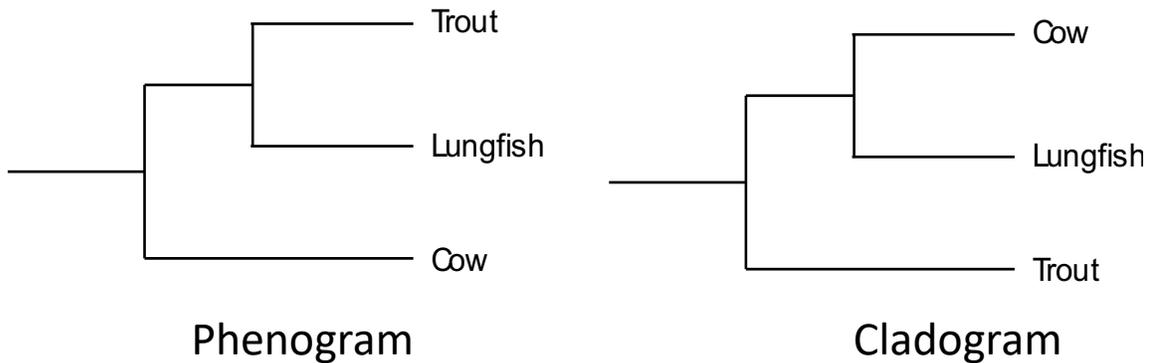
Hennig's view was that it is in fact possible to infer common ancestry in a scientific manner.

Attributes that are **derived (apomorphies)** and **shared (Synapomorphies)** by a set of taxa are *prima facie* evidence for exclusive common ancestry.

Thus, the goal of cladists is to uncover monophyletic groups (clades) by finding synapomorphies.

Only derived characters (**apomorphies**) can be phylogenetically informative, so in the Hennigian approach, the first step is to determine which character states are derived and which are primitive.

One of my favorite simple illustrations of the differences between phenetics and cladistics is that of a Cow, a Trout, and Lungfish (it sounds like a bad joke...).



The Hennigian approach is based on identifying synapomorphies that define a group. The presence of limbs (rather than fins) is a synapomorphy.

However, if we look at many characters, there will be conflict. The only methodology that is permissible to cladists to resolve such conflicts is the method of **maximum parsimony**. That is, the tree that requires the fewest evolutionary steps is to be preferred. We'll address parsimony as an optimality criterion in great detail later.

Early cladists such as J.S. Farris and Arnold Kluge demonstrated that **the MP tree is that tree which maximizes synapomorphies**, and therefore is the tree on which groups are defined by shared derived characters to the greatest extent possible. That is, the MP tree defines groups following Hennig's principles. Thus, some cladists viewed MP as the only justifiable means for distinguishing among possible trees.

Pattern Cladists – A movement arose among cladists in the 1980's that parsimony trees, or cladograms, merely represent the pattern of character variation in the data rather than an actual phylogeny. Although this movement was, to a large degree, squelched by non-pattern cladists, elements of pattern cladism certainly persist.

“Although the assumption of evolution is sufficient to justify cladistics, it is also sufficient to justify competing approaches like maximum likelihood, which suggests that the philosophical support for the cladistic approach is strengthened by purging reference to descent with modification altogether (Brower. 2000. Cladistics 16:143).”

The view has lingered (Ebach et al. 2013. Zootaxa 3641:587), as have over-the-top reactions to it (Farris. 2014. Cladistics 30:236).

The term "cladist" is loaded in that it has many possible definitions. Quinn (2017 - pdf on course website) identifies seven that may be gleaned from the literature.

D. Statistical Phylogenetics – In spite of the view among many cladists that statistical approaches to phylogeny are anathema, Cladistics has a distinctly statistical origin that Joe describes in Chapter 10. Especially relevant were the pioneering works of Anthony Edwards, and Felsenstein himself has certainly been one of the most influential and important proponents of statistical phylogenetics.

As we discussed the other night, the perspective that phylogenetic analysis is a statistical endeavor languished in the shadows for a couple decades.

Nevertheless, the dominant paradigm in phylogenetics currently is that phylogenies are estimated with uncertainty and that one must quantify that uncertainty.

We can look at the above example (trout, lungfish and cow) under the statistical approach.

We have these alternative trees, and we could take either a frequentist or a Bayesian approach to evaluating them. For example, we could force the data to fit them both and see if one fits the data significantly better than the other. If that's the case, we can reject one of them.

Because statistical inference requires a model, this school tends to rely on model-based methods such as **maximum likelihood** and **Bayesian** estimation.

Cladists have attacked the new school with the same animosity that they attacked phenetics in the 70's.

Cladists retain resistance to statistical approaches. This is apparent in the Schuh and Brower book, as well as the social media storm over "ParsimonyGate" 8 years ago.

See a summary at: <https://www.wired.com/2016/02/twitter-nerd-fight-reveals-a-long-bizarre-scientific-feud/>