

## Fossils in Classification

“Fossils are so incomplete that cladograms should be based on recent groups alone and fossils (if any) should be added into appropriate stem lineages after the fact.”

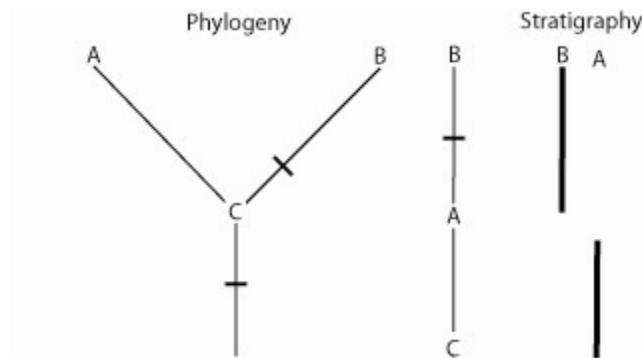
(Ax 1987)

“The inclusion of fossils in cladistic analyses can substantially alter inferred relationships among extant groups and/or ideas on character evolution. We suggest that every effort be made to incorporate them from the beginning.”

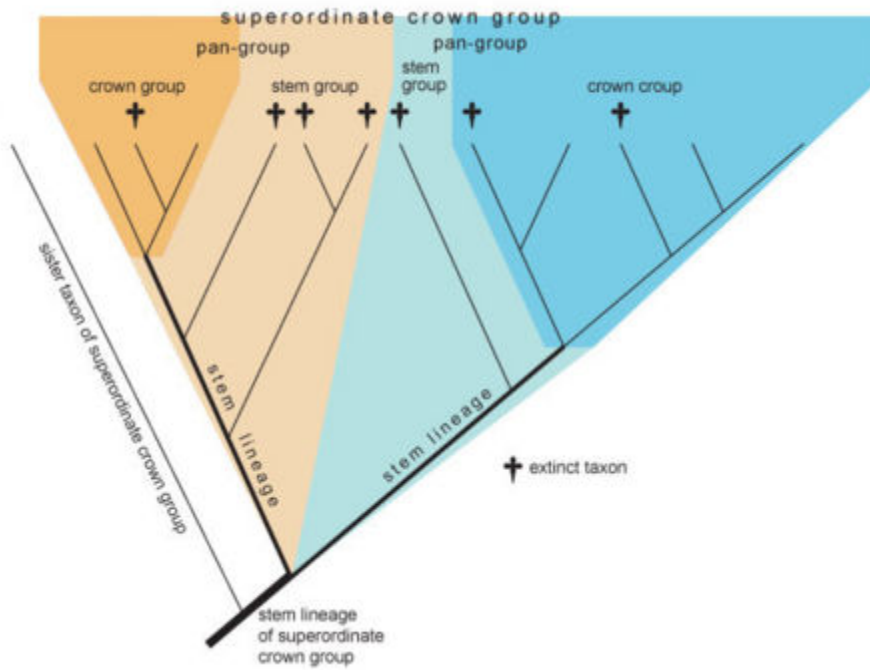
Donoghue et al. (1989)

During much of the 19th and 20th centuries, palaeontology was often considered as fundamental for understanding relationships among extant taxa. Then, in the late 1970s and early 1980s, with the advent of cladistics, the supremacy of fossils in phylogentic reconstruction was forcefully and successfully challenged by a paleontologist! Colin Patterson (1981):

- (1) The distribution of traits among extinct taxa could be used to estimate sister group relationships, but the incompleteness of fossils makes fossils inherently less informative than extant taxa. Thus as a practical matter including fossil data will rarely make major contributions to phylogeny reconstruction.
- (2) Fossils can be used to determine ancestor-descendant relationships. But suppose that species A and B are “sister taxa,” and all of A’s traits are ancestral relative to B’s, and species A both appears in and disappears from the fossil record before B. Would this justify the claim that A is the ancestor of B? While it is possible that A evolved directly into B, it is also possible that A and B are sister species that diverged from a common ancestor (C).



Patterson concluded “...that the widespread belief that fossils are the only, or best, means of determining evolutionary relationships is a myth.”



Edgecombe (2010) “Twenty years have passed since it was empirically demonstrated that inclusion of extinct taxa could overturn a phylogenetic hypothesis formulated upon extant taxa alone, challenging Colin Patterson’s bold conjecture that this phenomenon ‘may be non-existent’. The exclusion of fossils from phylogenetic analyses is neither **theoretically** nor **empirically** defensible.”

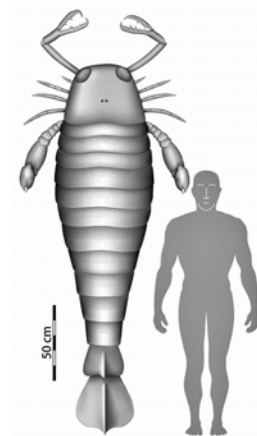
If 99% of all species are now extinct, failure to sample fossils is a huge loss of vast tracts of character space. How do we even imagine the Tree of Life without fossils much less reconstruct it?



Scorpions



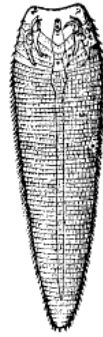
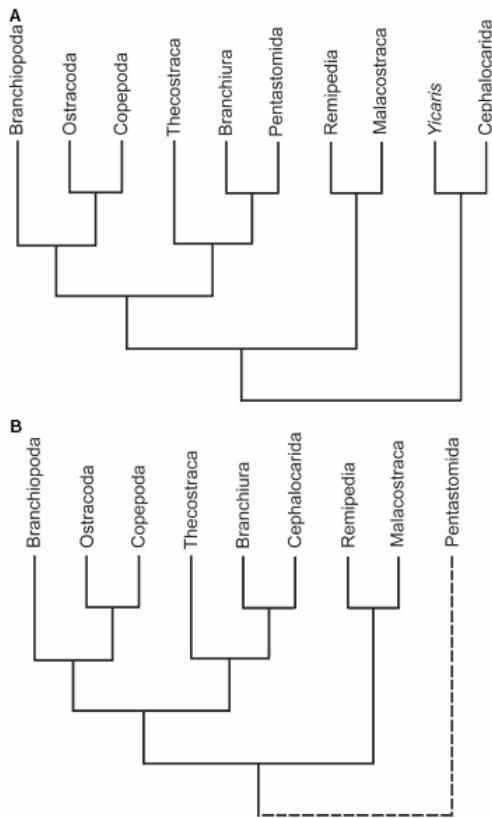
Horseshoe Crabs



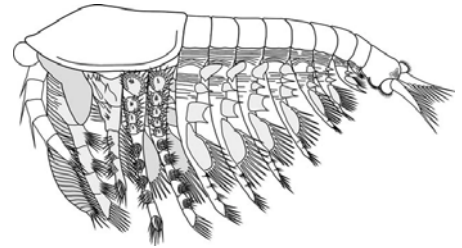
Eurypterids †

In zoology - vertebrate workers have been more likely to incorporate fossils into their analyses than invertebrate worker. Surprising?

Gauthier et al (1988) analysis of amniote relationships was one of the first empirical demonstrations that a cladogram constructed without fossils could be overturned by their inclusion and inspired a renewed exploration of how fossils impacted on cladistic analyses using real data sets rather than guesswork and anecdotal phylogenies.



Pentastomids



*Yicaris*

Typically, parsimony costs of a hypothesis (or classification) are altered by unique character combinations in fossils.

1. Fossils break up long branches (by having some but not all derived characters of the crown-group members of a clade),
2. Fossils help root trees because some characters can be homologized with fossil outgroups that cannot be homologized with modified **extant** taxa.
3. Fossils can help to determine character polarities that were ambiguous in their absence.
4. Fossils are often useful in sorting out character conflicts where internodes are short and terminal branch lengths are long, as is the case when the living diversity of a clade has been pruned by extinction and is only a subset of a much richer extinct diversity.
5. Fossils may provide fundamentally different hypotheses of homology (not necessarily effects classification).
  - a. Example, fusion of palate and the braincase of tetrapods and lungfish. Synapomorphy of the Choanata or independently acquired in each group?

- b. Clusters of character acquisition linked to genome duplications in vertebrates disappear with the addition of fossil taxa, which instead expose a nested hierarchy of characters.

**How does one add fossils to an analysis?**

Molecular dating models typically map fossil onto phylogenetic trees without having them in the original analysis. What is considered is:

1. quality of preservation
2. identification (reliability of the taxonomic placement)
3. Accuracy of the published age

“The tendency to map fossils onto phylogenetic trees without including them directly in analyses makes the original identifications and quality of the fossils used extremely important. Although it is refreshing to see that fossils are utilized by molecular biologists to date their trees, it is also disappointing to see that sometimes they do not consider several issues when selecting fossils to be used as calibration points. Most will agree that merely mapping fossils on trees is not optimal because such placements are not directly tested and are, therefore, subjective.”

Gandolfo et al. (2008)

Many biogeographic studies also use fossils to provide historical distributional data, but here again the fossils are usually not included in the original analyses and are simply mapped onto phylogenetic trees based on the identification of the fossil.

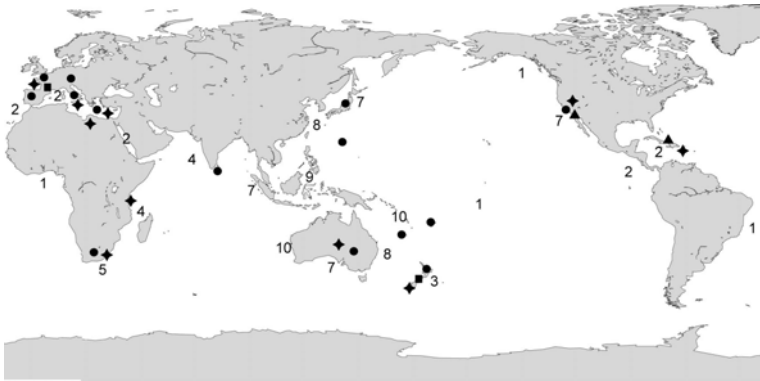
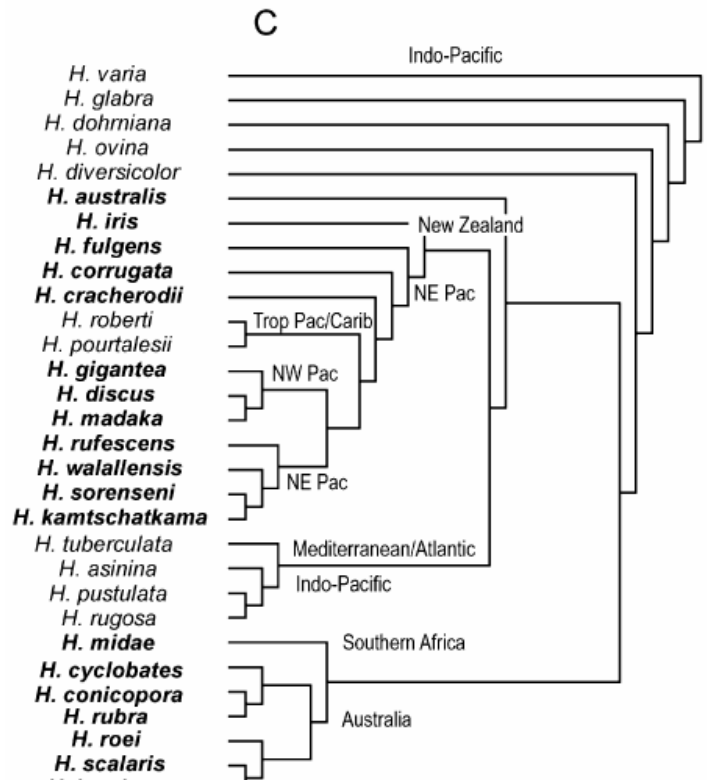


FIGURE 1. Worldwide distribution of living and fossil abalone. Numerals indicate approximate number of living species in each region. Distributional data from Geiger (1998, 2000); fossil data from Geiger and Groves (1999).



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The most problematic aspect of poor reconstructions, fossil misidentifications, and taxonomic misplacements results from the use of suspect fossil data by non-experts in studies that utilize fossil occurrences to estimate ages of clades. If the fossils were too fragmentary to be included in the phylogenetic analyses in the first place – how can they later be mapped on to a result of an analysis? Why is it now okay to accept the original description, taxonomic assignment, and geologic dating without further investigation?

If the fossil taxon has not been previously included in a phylogenetic analysis, it should be include into a morphological analysis of extant taxa that are within the scope of the identification and the study group – whether molecular or morphological.

And the technology to extract and reconstruct fossils is getting better and better ...

