

### Integrating Fossils into Phylogenies

Throughout the 20th century, the relationship between paleontology and evolutionary biology has been strained.

Two common answers are:

- (1) the two fields have fundamentally different aims, and
- (2) the tensions arise out of disciplinary squabbles for funding and prestige.

Principal differences between neontology and paleobiology

	Neontological evolutionary biology	Evolutionary paleobiology
Focus of study	Living organisms	Fossil remains of organisms
Temporal perspective	Shorter term: $10^{-2} - 10^3$ years	Typically longer term: $10^3 - 10^7$ years
Theory	Models of natural selection and Speciation, generally articulated in terms of population or quantitative genetics	Relies on broader neo-darwinian theory; rarely uses population genetic theory. Some distinctively paleobiological theory (e.g., taphonomy)
Methods	Greater emphasis on experiments	Less emphasis on experiments
Data	Emphasizes genetic data and population structure	Extremely limited access to genetic data and population structure

John Maynard Smith (1920-2004) – British evolutionary biologist and geneticist; evolution of sex, game theory in evolution, and signaling theory.

Smith, J. M. (1984). "Paleontology at the high table." *Nature* 309 (5967): 401-402.

Hennig – *Character phylogeny* (polarity).

“Criterion of geological character precedence. If in a a monophyletic group a particular character condition occurs only in older fossils, and another only in younger fossils, then obviously the former is pleisomorphic and the latter the apomorphic condition.”

Hennig goes on to discuss paleontological methods of phylogenetic systematics.

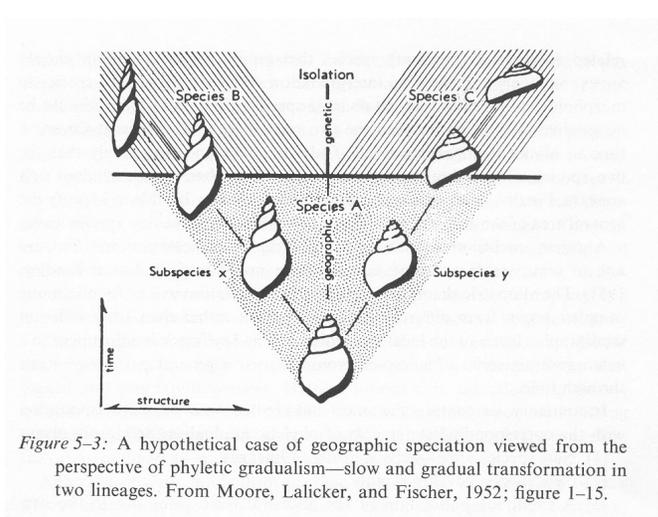
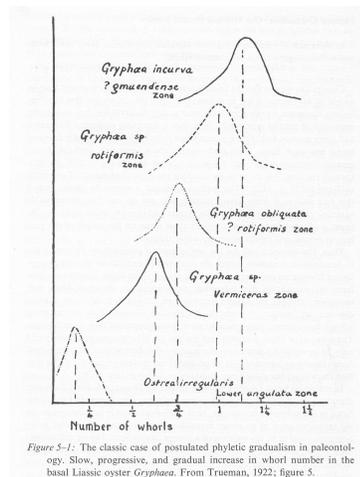
During much of the 19th and 20th centuries, palaeontology was often considered as fundamental for understanding relationships amongst extant taxa. . . . Then, in the late 1970s and early 1980s, with the advent of cladistics, the supremacy of fossils in phylogenetic reconstruction was forcefully and successfully challenged. 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. In addition he argues that in practice. 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 concludes “that the widespread belief that fossils are the only, or best, means of determining evolutionary relationships is a myth”

Patterson, C.: 1981, ‘Significance of Fossils in Determining Evolutionary Relationships’, *Annual Review of Ecology and Systematics* **12**, 195–223.



Resolution of long branches: Burgess Shale Arthropods.

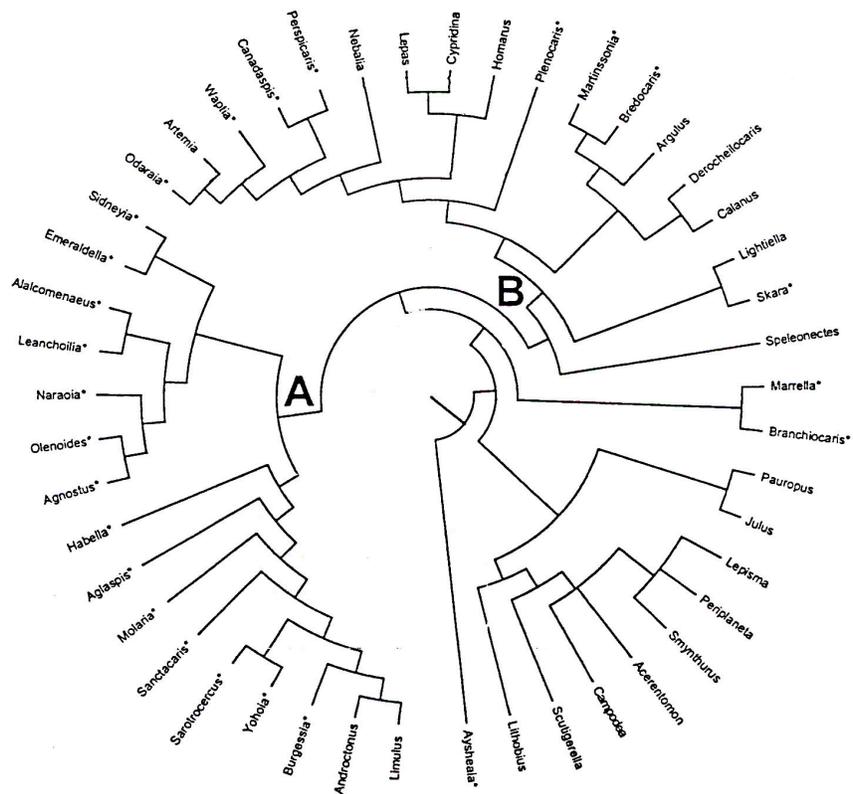
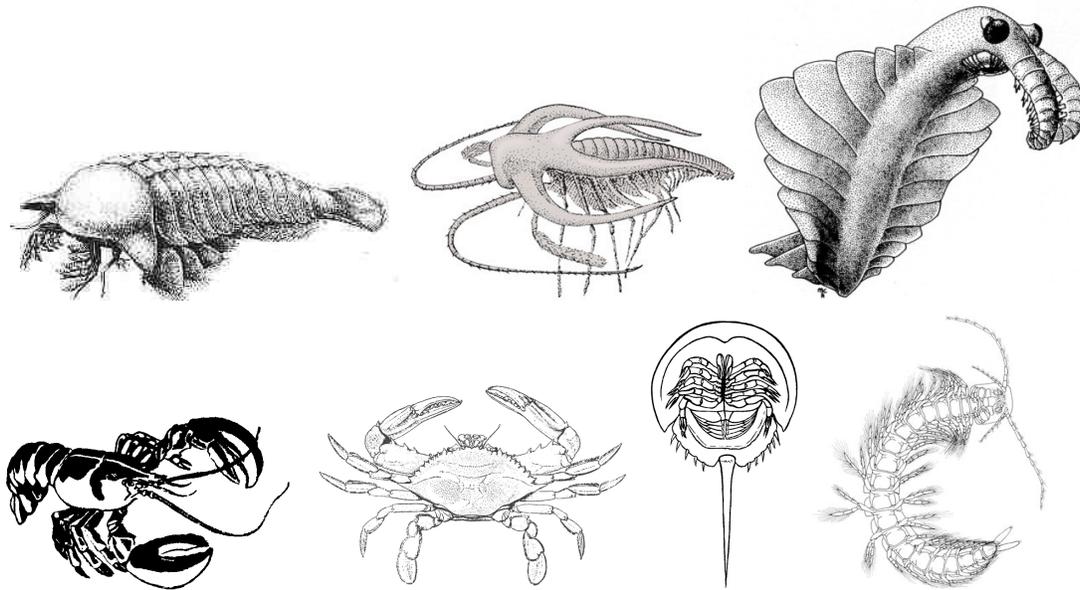


Figure 2 Cladogram of Cambrian and living arthropods. Cambrian arthropods are marked with an asterisk. In subclade A 87.5% of the taxa are extinct Cambrian taxa; in subclade B only 44.4% of the taxa are extinct. Differential extinction rates in different subclades exacerbate patterns of disparity. After Briggs et al (1992).

Recent reviews suggest that fossil data are useful to:

- (1) determine the polarity of specific traits or to identify the root of an unrooted tree.
- (2) provide a more detailed reconstruction of the sequence of evolutionary changes that led to novel traits.
- (3) re-assess initial hypotheses of homology or homoplasy.

Although evolutionary systematics initially created a rift between paleobiological and neontological systematists, cladistics ultimately provided a set of methods that have been broadly accepted in both communities. Thus, the “cladistics revolution” contributed to the methodological unification of these fields.

### Stratigraphic Data

Cladistic analyses can conflict with the temporal information provided by the fossil record. Suppose that a cladistic analysis supports the hypothesis that A is the sister taxon to (BC). This analysis implies that A (or the lineage from the common ancestor of all three taxa to A) must have existed before the appearance of either B or C. What if A does not enter the fossil record until well after B and C? Is this evidence against the cladistic inference?

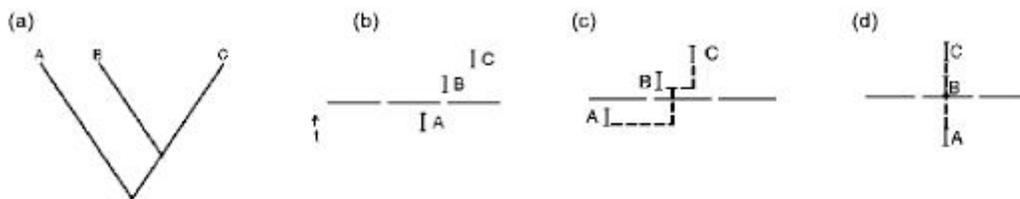


Figure 3. Alternative Approaches to Constructing Trees. A cladogram depicting the relationship between taxa A, B, and C (shown in 3a) can be combined with the stratigraphic information (b) in two distinct ways, resulting in two different trees (c and d).

Three responses to the integration of stratigraphic data into the fossil record.

- (1) *Strict cladism* relies solely on character data to determine the pattern of branching. Conflicts between stratigraphic and character data are thought to result from incompleteness in the fossil record.
- (2) *Limited use of stratigraphic data*. Stratigraphic data can be used as a tiebreaker to decide between equally parsimonious cladograms (or to infer a tree from a cladogram), but are never allowed to “over-ride” parsimony considerations. Primarily associated with Andrew Smith (BMNH)
- (3) *Full incorporation of stratigraphic data*. Several different methods attempt to estimate phylogeny in light of *both* stratigraphic and character

data. These methods sometimes accept less parsimonious cladograms in order to gain better stratigraphic fit.