

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. □

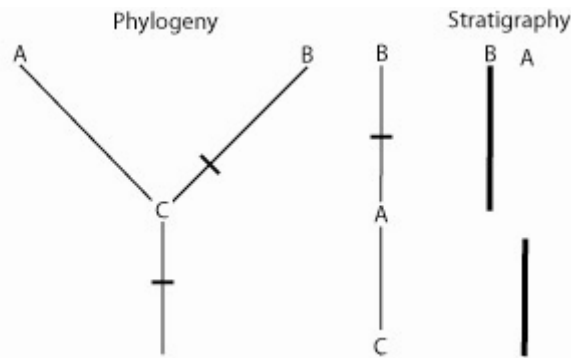
Hennig – *Character phylogeny* (polarity).

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

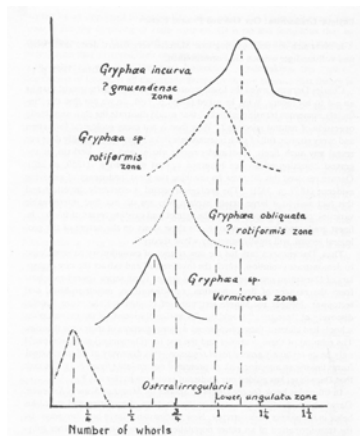


Figure 5-1: The classic case of postulated phyletic gradualism in paleontology. Slow, progressive, and gradual increase in whorl number in the basal Liassic oyster *Gryphaea*. From Treutman, 1922; figure 5.

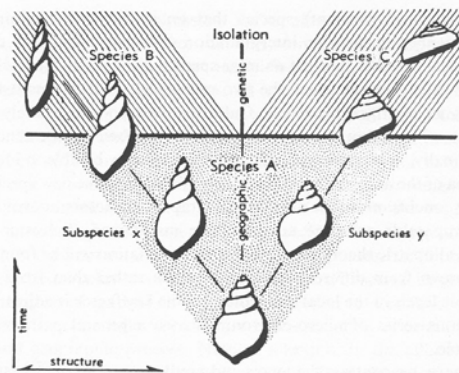


Figure 5-3: A hypothetical case of geographic speciation viewed from the perspective of phyletic gradualism—slow and gradual transformation in two lineages. From Moore, Lalicker, and Fischer, 1952; figure 1-15.

Resolution of long branches: Burgess Shale Arthropods.

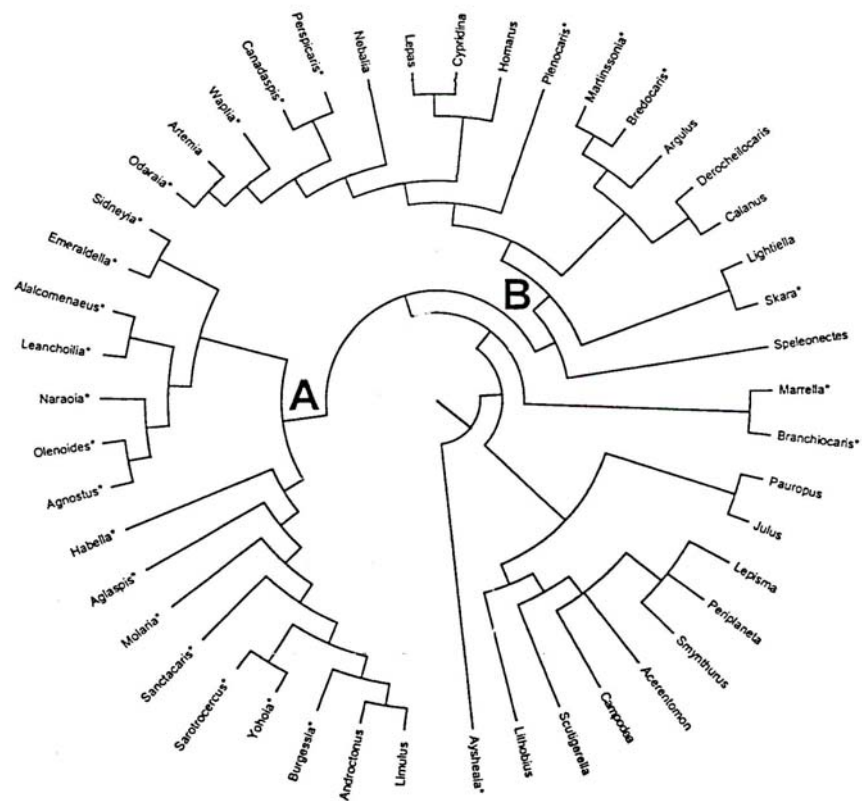
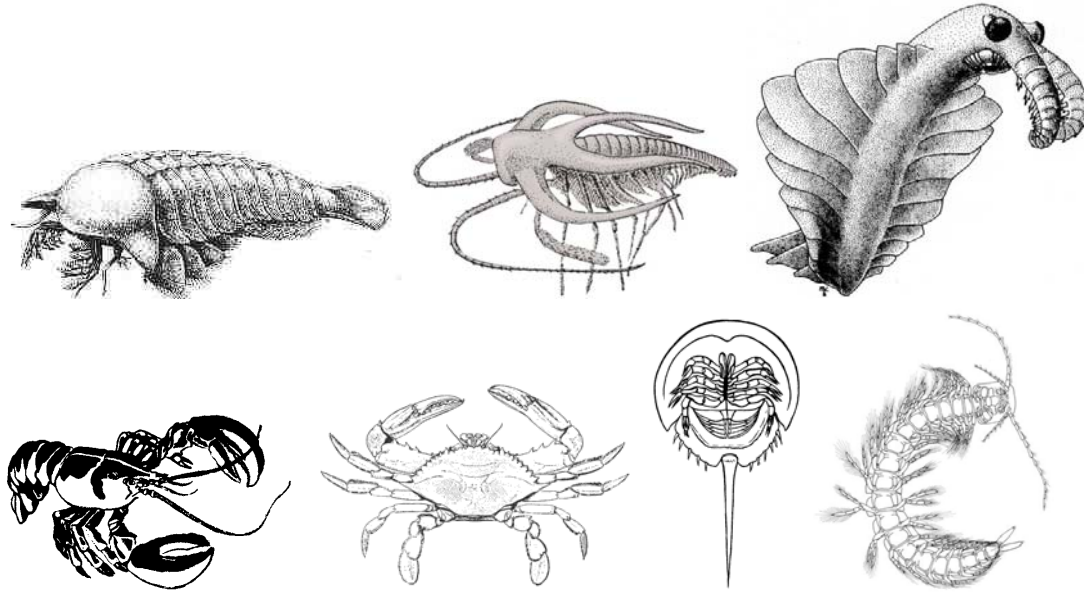


Figure 2 Cladogram of Cambrian and living arthropods. Cambrian arthropods are marked with an asterisk. In subclade A 87.5% of the taxa are extinct Cambrian taxa; in subclade B only 44.4% of the taxa are extinct. Differential extinction rates in different subclades exacerbate patterns of disparity. After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

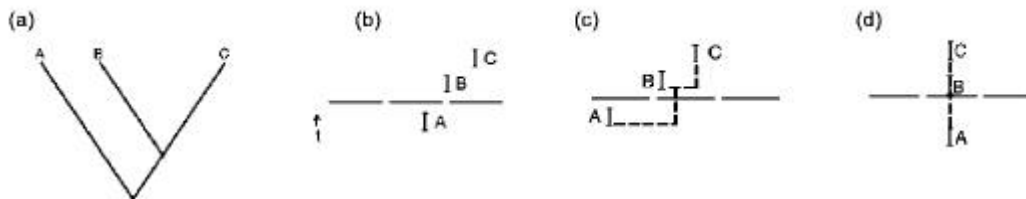


Figure 3. Alternative Approaches to Constructing Trees. A cladogram depicting the relationship between taxa A, B, and C (shown in 3a) can be combined with the stratigraphic information (b) in two distinct ways, resulting in two different trees (c and d).

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.

Number 1 requires ad hoc assumptions about the fossil record. If you want to avoid ad hoc assumptions in your research then it makes sense to use stratigraphic evidence as a “tiebreaker” (i.e., to decide among equally parsimonious cladograms)

Number 2 - Tie-breaker (Andrew Smith BMNH)

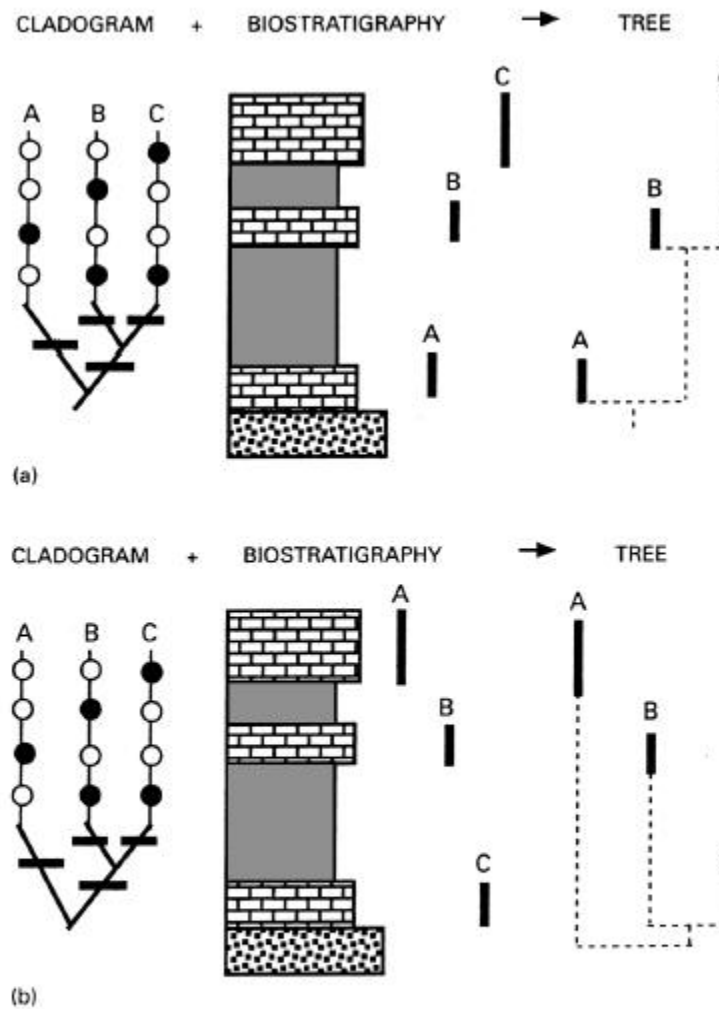


Figure 4. Simple Illustrations of Smith's Method. (a) and (b) provide two simple illustrations of Smith's method. When all taxa are supported by unique derived traits, the evolutionary tree must maintain the branching pattern of the cladogram, even if this requires range extensions and ghost lineages. See text for further explanation. Reprinted with permission from Smith (1994).

Stratophenetics (Phil Gingerich UM)

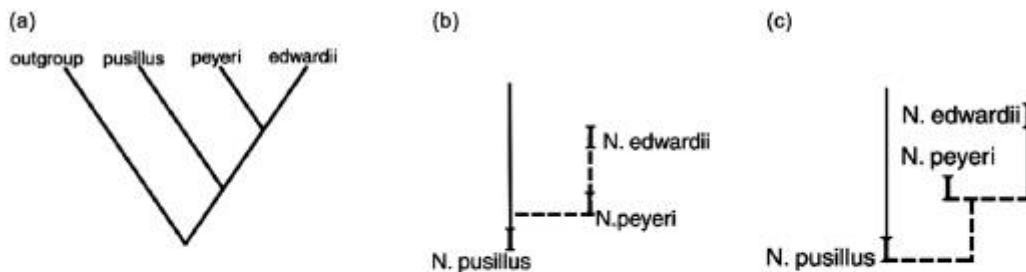


Figure 6. Reconstructing Pachypleurosaur Phylogeny. O'Keefe and Sander (1999) discuss two alternative trees ways to convert the cladogram (a) into a tree: a "stratophenetic" tree which allows stratigraphic information to override weak parsimony considerations (b) Smith's more cladistic approach (c).

Stratophenetics favored by O'Keefe and Sander because:

- (1) The species are stratigraphically non-overlapping; they are never found together.
- (2) 400 specimens were identified in this basin, including many complete skeletons. Given this quality of preservation, extending the range of *N. edwardsii* back in time (as in 6c) is an ad hoc assumption of incompleteness.
- (3) These two species are endemic to this basin. Appearance in the basin probably reflects a real origination (not immigration) and their disappearance is best seen as either extinction or anagenesis (not emigration).

Number 3 - Full incorporation of stratigraphic data (Dan Fisher UM, Pete Wagner USNM, Ken Angielczyk IB & UCMP)

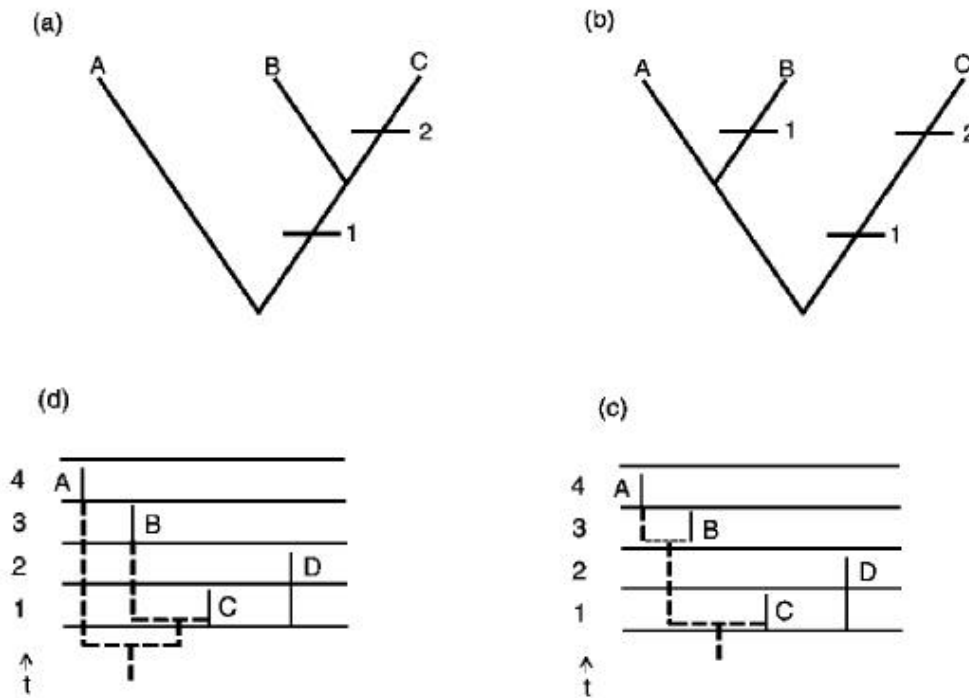


Figure 7. An Example of Stratocladistic Reasoning. Even though cladogram (a) is more parsimonious than (b), the evolutionary tree shown in (c) has a lower total “parsimony debt” (i.e., character debt + stratigraphic debt) than (d). As a result, stratocladistic approaches allow stratigraphic evidence to over-ride character-based parsimony.

The stratigraphic debt is equal to the number of intervals through which lineages must be extended, even though other species in the clade were observed during those intervals. This technique applies to range extensions and ghost lineages, but not to unobserved intervals within the duration of the species. Based on the character matrix alone, parsimony favors A(BC) over (AB)C.

Stratocladistics reverses this preference, based on the total parsimony debt of the two trees.

(AB)C has 3 units of stratigraphic debt (the range extension of A plus the ghost lineage leading to (AB)). (AB)C has a total parsimony debt of 4: 1 homoplasy + 3 units stratigraphic debt. A(BC) has 5 units of parsimony debt: 0 homoplasies + 5 units of stratigraphic debt. Thus substantial gains in stratigraphic fit (49%) can be realized without significant loss (4%) in morphologic fit.

BUT, How many intervals of unobserved fossil lineages does it take to equal one homoplasy? Also, by subdividing stratigraphic intervals more finely, one can increase the weight given to stratigraphic data

Wagner addressed the problem by using a maximum likelihood to provide a common currency for “weighing” stratigraphic and character debt. The method rests on one central idea: when two independent data sets (A and B) are available, the likelihood of an outcome O is given by the

following formula: $L(O) = L(O|A) \times L(O|B)$. Thus, assuming that character data and stratigraphic data are independent, the likelihood of any given phylogenetic tree (PT) is given by the formula:

$$L(\text{PT}|\text{all data}) = L(\text{PT}|\text{character data}) \times L(\text{PT}|\text{stratigraphic data})$$

BUT, Wagner's simulations involve small (six species) clades and he did not determine whether the results were statistically significant from other methods. Second, it is not clear whether we can reliably estimate $L(\text{PT}|\text{character data})$. One can only assess the likelihood of a phylogeny relative to a model of character evolution. It is not clear, however, that we have adequate models of character evolution.

Lastly,

Angielczyk & Fox analyzed 550 simulated data sets using cladistics and stratocladistics. They found that the absolute difference in fit to stratigraphy between the results of the two methods was strongly correlated with the probability of character state transition and the accuracy of the stratocladistic results relative to the cladistic results. Completeness of the fossil record and number of taxa included in the analysis were only weakly correlated with stratigraphic fit. Their results suggest that measuring the difference in stratigraphic fit between cladistic and stratocladistic trees might be useful to qualitatively estimate whether the addition of stratigraphic data benefits a phylogenetic analysis, and for identifying data sets with high average rates of character state change.

Angielczyk, K. D. and Fox, D. L. 2006. Exploring new uses for measures of the fit of phylogenetic hypotheses to the fossil record. *Paleobiology* **32**: 147-165.

This started in Phylogenetics 200A as Ken's class project!