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COMMENT

The logically consistent relationship between cladograms and synapomorphies

Here I explore the biological relevance, origin and meaning of the concept of cladogram (rooted, directed branching diagrams representing the hypothesized phylogenetic relationships among the terminal taxa under study) and argue that cladograms do not necessarily entail synapomorphies, but synapomorphies are required to test and ultimately falsify cladograms. Both cladograms and synapomorphies are required to achieve phylogenetic explanation. I conclude that within a phylogenetic, scientific context, testability refers to the logical relationship among cladograms (hypotheses), synapomorphies (evidence), and background knowledge (descent with modification). It is the relationship between evidence and hypothesis that underlies a logically consistent relationship between synapomorphies and cladograms. The capacity of a given cladogram, as a hypothesis, to explain synapomorphies complements this relationship and conforms phylogenetic explanation.

1 Biological relevance of cladograms

Knowledge of phylogenetic relationships among extant and extinct organisms is paramount for understanding the evolutionary processes involved in the diversity of life. Detailed knowledge of phylogeny is necessary to explain the evolutionary origins of features and provides an essential predictive framework to guide research. Phylogenetic tools allow us to identify natural groups of organisms and how they are related to each other (Donoghue *et al.*, 1989; Grant *et al.*, 2006).

Observed biodiversity demands explanation. Heritable variation at the levels of DNA and phenotype provides the evidential basis for formulating and testing phylogenetic explanations (hypotheses, *i.e.*, cladograms). The fundamental objective of phylogenetic analysis is to explain biological variation by inferring evolutionary relationships among organisms and the unique transformation events, or synapomorphies, that link them (Hennig, 1966). Although evolutionary analysis requires additional assumptions and tests external to the phylogeny, inference of functions, mechanisms of adaptations, and constraints, and other processes that shaped the evolution of biological groups, can be informed by the results of phylogenetic analysis (Wheeler *et al.*, 2006). The novel knowledge that emerges from phylogenetic reconstruction has implications beyond the immediate problems of systematics. By providing a relevant framework of reference, knowledge of phylogeny often leads to unanticipated insights and identifies novel problems for further investigation (Grant *et al.*, 2006; *e.g.*, biogeography and character evolution). Further, observed biodiversity demands not only explanation, but also documentation, and improved knowledge of phylogeny facilitates taxonomic work by highlighting relevant comparisons. Progress in taxonomy forms the foundation for future research in diversity.

2 Discussing the concept of cladogram

Brower (2016) timely reviewed the origin, meaning and use of the term “cladogram”, a concept that, similarly to that of a “phylogenetic network” (discussed by Kong *et al.* (2016); and citations therein), has been used indiscriminately in the literature. I agree, as would most phylogeneticists, with two of Brower’s general points. First, “cladogram” has been defined, in general, “as a graphical representation of an empirical hypothesis of relationships among taxa”. Whether this representation of a hypothesis of relationships is “based on evidence from synapomorphies alone” (p. 573; abstract) or not will be discussed below. And second, one would certainly expect that after almost 60 years of post-Hennigian debate, clear and unambiguous terminology would have been reached in the current literature on phylogenetic inference. Yet this is not the case. As correctly pointed out by Brower, many evolutionary biologists use the terms “phylogeny”, “tree” (either evolutionary and phylogenetic trees or tree graphs), “cladogram” and, I would add, non-phylogenetic “networks” (see Kong *et al.*, 2016, 2023; Sánchez-Pacheco *et al.*, 2020) interchangeably, thereby confusing their meaning. Similarly, other authors

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(*e.g.*, Wägele, 2005; Parenti & Ebach, 2009) conflate "cladogram" with "phenogram", "phylogram" and "dendrogram"[1] without any consideration of the theory behind the concepts. Therefore, Brower called for retaining the "historical meaning" of the word "cladogram" (p. 575). But what is that historical meaning of "cladogram"? In his valuable contribution, Brower overlooked several key points, which I address below.

Brower's (2016) main premise is quite clear: a cladogram implies relative recency of common ancestry, as evident from the presence of, or based on evidence from, synapomorphies alone (pp. 573–574). In other words, synapomorphies are a requisite of cladogram (hereinafter "synapomorphy ∊ cladogram"). From the logic of phylogenetic analysis, here I discuss the legitimacy of Brower's claim, further explore the historical concept of "cladogram", and argue that the only logically consistent relationship between cladogram and synapomorphy is that cladograms do not necessarily entail synapomorphies, but synapomorphies are required to test and ultimately falsify cladograms. And both cladograms and synapomorphies are required to achieve phylogenetic explanation.

3 Absence of synapomorphies in (sub)cladograms, and the concepts of cladogram and optimal cladogram

After quoting and commenting Hennig (1966, pp. 194, 196) and a series of definitions of "cladogram", Brower (2016) concluded (p. 574, italics added):

> [A] cladogram is a special sort of dendrogram, depicting an empirically supported hypothesis of branching order that implies relative recency of common ancestry, as evident from the presence of shared, derived character states (synapomorphies), and which does not take into account degree of similarity or difference, branch length or absolute time. *So what's the problem?*

In Hennig's sense, phylogenetic relationships are represented as nested sets of sister-groups only (Wheeler, 2012). This is included appropriately in Brower's definition of cladogram (in terms of recency of common ancestry, as evidenced by the shared presence of derived character-states, *i.e.*, synapomorphies). *The problem is* that, under a framework of refutation and corroboration of phylogenetic hypotheses, even in instances where it is not possible to claim the existence of any kind of hypothesized hierarchical branching order (*i.e.*, nested sets), "there remains the completely unresolved proposition, the *trichotomous* [sub]*cladogram* (*i.e.*, polytomy) in the potentially informative simplest case" (Kluge, 1997; p. 86, emphasis added). Consider the same three-taxon example of A, B, C provided by Brower (p. 573) and in detail by Kluge (1997, p. 87; 2003, p. 236). If a set of putative synapomorphies are distributed as 110, 101, and 011 (where character state 0 is plesiomorphic and character state 1 is apomorphic), respectively, then three equally optimal rooted cladograms exist when conjoining the solutions with the congruent and incongruent synapomorphies: $((A_1, B_1)\ C_0)$ or $((A_1, C_1)\ B_0)$ or $(A_0\ (B_1, C_1))$, where parentheses indicate relative recency of common ancestry. In each cladogram, the derived character-states of the incongruent synapomorphies are explained by independent transformation events. For example, for the cladogram ((A, B) C), the taxonomic distribution of the incongruent synapomorphies is $((A_1, B_0)\ C_1)$ and $((A_0, B_1)\ C_1)$, respectively. There remains, however, the completely unresolved, rooted cladogram, (A B C), as a competing (though less parsimonious, for example) hypothesis. And what about a strict consensus cladogram? The strict consensus includes only clades that are unambiguously supported by the available evidence (Grant & Kluge, 2003, 2008). However, in this example equally optimal solutions contradict all monophyletic groups, and a complete polytomy depicts the summarized objective knowledge of relationships (Grant *et al.*, 2003). Consequently, polytomies may not be nested sets of sister-groups based on synapomorphies but are still competing explanations of relationships. Within the logic of testability, therefore, cladograms are better defined conceptually as *directed branching diagrams representing the hypothesized phylogenetic relationships among the terminal taxa under study*, and thus *optimal cladograms* are to be inferred from a character-based analysis, *e.g.*, by minimizing the character transformation events required to explain the observed variation of the evidence, which is delimited in transformation series *sensu* Hennig (1966; Grant & Kluge, 2004). As evidenced in the cases of polytomies, the statement "synapomorphy ∊ cladogram" does not hold in all instances of "[sub]cladogram".

4 Origin of the concept of cladogram

The Wagner method (Farris, 1970) uses character optimization to minimize the number of character transformation events (*i.e.*, a character-based method). The approach uses the patristic distance (character-state transformations, steps, diagram length) of a phylogenetic hypothesis to explain the observed character variation (Farris, 1967; Kluge & Grant, 2006).

[1] I do not mean to review these particular concepts, except for "cladogram". Instead, readers are referred to the relevant literature. For instance, Wheeler (2012) offers an excellent compilation of clear definitions (*e.g.*, graph, tree, network), and Brower (2016) himself provides some succinct meanings (*e.g.*, phenogram).

In Wagner networks (undirected branching diagrams), the set of nodes includes both the observed taxa (operational taxonomic units, OTUs) and the hypothetical taxonomic units (HTUs). The associated branches connect them with using transformation events to produce a Wagner tree (directed branching diagrams). The difference lies basically in the optimization and polarity of character-state transformations as determined by the absence (network) or presence (tree) of rooting (but see below for consequences in evolutionary inference). Formation of a hierarchical branching order (*i.e.*, nested sets of sister groups) is a consequence of the direction given when rooting the branching diagram. Therefore, Wagner networks cannot be nested sets of sister groups based on synapomorphies. Although Farris (1970) did not use the term cladogram as such—branching form (dendrogram) instead, the concepts of "cladistic" and "cladogram" were first given a cladistic treatment (*i.e.*, a methodology based on character transformation events instead of similarity, the Wagner method) by Farris (*contra* Williams & Ebach (2008, p. 5)). Nevertheless, the theoretical foundations of these concepts, as implemented in character-based methods, trace back to Wagner (1961), who first proposed the procedure upon which Farris (1970) built the Wagner method. Likewise, Farris (1967) recognized cladistic relationships (cladogenic events, topology, and hypotheses of monophyly) and patristic relationships (character-state transformation events and hypotheses of homology), thus defining conceptually the problem of phylogenetic explanation (Kluge & Grant, 2006).

5 The logical relationship between cladogram and synapomorphy

Phylogenetic explanations are definitionally historical and, therefore, entail directed cladograms (Wheeler *et al.*, 2006). Outgroup comparison roots the topology and polarizes character transformations (Farris, 1972, 1982). This action converts a non-evolutionary network, in the sense that it lacks ancestor–descendant relationships, as well as representations of sister-group relationships, into an evolutionary hypothesis, *i.e.*, a phylogenetic tree. In phylogenetic trees, the nodes signify both sister-groups and ancestral conditions, and the branches that connect them contain the character transformations between ancestors and descendants (Nelson, cited in Eldredge & Cracraft, 1980; Wheeler, 2012). As such, the evolutionary history of the characters and the organisms can only be inferred by ordering terminals, explaining characters, and testing hypotheses on phylogenetic trees (Wheeler, 2012).

Within this phylogenetic, scientific context, testability refers to the logical relationship between cladograms (hypotheses), synapomorphies (evidence), and background knowledge ((descent with modification *sensu* Darwin (1859)) (Kluge, 1997, 1999, 2003). Of particular interest here is the relationship between cladogram and synapomorphy. According to Kluge (1997, p. 82), falsifying cladograms through synapomorphies is "consistent with the logic of Popperian testability and its practice of refutation and corroboration (Popper, 1968, 1992)". Therefore, it constitutes a form of hypothetico-deductive testing. Synapomorphies are evidence because only these empirical relations have the potential to refute (falsify) cladistic hypotheses (cladograms) [2] (Hennig, 1966; Kluge, 1997, 2003). Refutation, however, lies in incongruent synapomorphies (explained as homoplasy), because these shared character-states imply evidence for a different, competing cladogram (see the three-taxon example above and Kluge (1997, 1999) for an expanded explanation). It is this relationship between evidence and hypothesis that underlies a logically consistent relationship between synapomorphy and cladogram. The capacity of a given cladogram, as a hypothesis, to explain synapomorphies complements this relationship (Kluge, 1999).

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[2]Note that polytomies, as hypotheses of relationships, are also testable with synapomorphies.

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