Evolution Is Not a Necessary Assumption of Cladistics

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Although the point has already been emphasized by various authors that the assumption of descent with modification is not required to justify cladistics, recent debate suggests that there is still confusion surrounding the necessary and sufficient background knowledge underlying the method. Three general axioms necessary to justify cladistics—the discoverability of characters, hierarchy, and parsimony—are reviewed. 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. © 2000

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"What we call the evolutionary hypothesis is an explanation of a host of biological and paleontological observations—for instance of certain similarities between various species and genera—by the assumption of the common ancestry of related forms." (Popper, 1957: p. 106)

"That is, the *making* of an inference does not require that characters be historically contingent, though this may be a 'problem' for making a 'true' inference, because we cannot know the truth, it is 'unproblematic.' " (Siddall and Kluge, 1997: p. 321).

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INTRODUCTION

At the 1997 Hennig meeting, Kirk Fitzhugh presented a talk entitled, "Cladograms as Explanatory Hypotheses," in which he claimed, among other things, that common ancestry is an inference rule for phylogenetic analysis—that is, that evolutionary theory provides a necessary underlying ontological basis for cladistics. Although that view was shown to be false more than a decade ago (Platnick, 1979, 1982, 1985; Nelson and Platnick, 1981; Patterson, 1982; Rosen, 1982; Brady, 1985), subsequent discussion among members of the audience revealed that substantial difference of opinion persists as to whether a theory of evolution is philosophically antecedent to systematics or systematics provides evidence that allows inference of a scientific theory of evolution. In this paper, I will advocate the latter point of view and highlight its utility in the current debate surrounding alternate methods of phylogenetic inference. Freeing cladistics from traditional assumptions of evolutionary background knowledge is an important epistemological step towards establishing a logically independent theory of systematics. To this end, I will review arguments based on the principle of parsimony developed some time ago by Farris, Platnick, Brady, and others that explain why the cladistic method is superior to phylogenetic inferential methods that rely on evolutionary assumptions.

HISTORY

Much of Hennig's (1950, 1966) motivation for developing his theory of phylogenetic systematics was a desire to counter the German school of "idealistic morphological systematics" that was prevalent in the first half of the 20th Century (e.g., Schindewolf, 1950). Those workers based inferences of relationship on similarity of form, considering phylogeny an irrelevant or derivative explanatory theory. Hennig's great insight was that although similarity occurs for several reasons (synapomorphy, symplesiomorphy, and convergence, the last having long been recognized as not indicative of relationship—see MacLeay, 1822), only special similarity (synapomorphy) is indicative of the pattern of phylogenetic relationship. Although Hennig (1966) dabbled with set theory as a rationale for the hierarchical arrangement of taxa using nested patterns of character transformation, his main defense for the approach of grouping by synapomorphy was based upon evolutionary process assertions. Hennig emphasized that his method depended on the ontological concept of hologenesis, an inductive extrapolation from the observed processes of development (ontogenesis) and sexual reproduction (tokogenesis) to the unobserved process held to be responsible for the hierarchical pattern of groups nested within groups (phylogenesis). This was more or less the same inductive argument developed by Darwin (1859: p. 433) to advocate the principle of evolution by natural selection as an explanation for the perceived hierarchical order of nature.

As discussed by Platnick (1979) and Nelson (1989), Hennig's metaphysical justification for grouping by synapomorphy alone is no longer necessary to explain the success of either systematics in general or the cladistic method in particular, yet it continues to be voiced with approbation at the meetings and in the publications of this society (e. g. de Queiroz and Donoghue, 1988, 1990; Frost and Kluge, 1994; Kluge, 1997; Siddall and Kluge, 1997). This is unfortunate, because the accusation of vague "evolutionary assumptions" in cladistics is often used to justify maximum likelihood (ML) methods, usually in the context of a statement such as, "(t)he model of evolutionary process is explicit in maximum-likelihood reconstruction, whereas it is largely implicit in other methods such as parsimony and neighbor joining" (Bull *et al.*, 1993: pp. 386–387), or

"despite the lack of an explicitly specified evolutionary model in parsimony analysis, there are reasons to believe that parsimony makes very stringent and unrealistic assumptions about substitution processes" (Yang and Goldman, 1998: p. 357). The object of this paper is to show that such claims are unfounded, by explicating the assumptions of the cladistic method and showing that evolution is not one of them.

BACKGROUND KNOWLEDGE AND PARSIMONY

At the 1997 Hennig meeting, Kirk Fitzhugh argued that scientific theories must rest on an ontology—an underlying view about the way things "really are" in nature. Since the demise of logical positivism (see Hanfling, 1981), no philosopher of science has tried to defend pure empiricism as a plausible methodology. However, there is an infinity of possible ontologies, so a simple corollary to the need for underlying ontological claims is that for a theory to be scientific, its ontology should correspond as closely as possible to available empirical evidence, that in turn rests on "common sense" background knowledge (Popper, 1979). Popper (1965: p. 238) defined the background knowledge underlying an hypothesis as "unproblematic" (cf. Siddall and Kluge, 1997), but this meant only that it was not the subject of immediate investigation in tests of the hypothesis, and definitely did not enshrine it as an article of faith immune to subsequent testing.

Parsimony is an epistemological approach (articulated by William Ockham more than 650 years ago; see Kluge, 1984; Rieppel, 1988) that restricts the realm of inferential reasoning to interpretation of evidence in the simplest theoretical framework necessary and sufficient to account for the data.[2] Extra background assumptions should be discarded, because they weaken the capacity of the empirical evidence to discriminate among competing theories. Popper (1959: p. 83) couched his argument for parsimony in the scientific method in terms of striving to avoid auxiliary

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[2]A source of confusion is the mistaken notion that cladists assume that systematic patterns are ontologically parsimonious—that character state-change is rare. Farris (1983) decisively refuted that claim.

hypotheses unless they increase the degree of falsifiability or testability of the main hypothesis. To facilitate the streamlining of background knowledge, Popper (1959: pp. 71–72) urged scientists to strive for the rigor of axiomatized systems—descriptions of their science reduced to minimally sufficient and necessary logical terms.

Various cladists have attempted to provide such systems for phylogenetic systematics. For example, Wiley (1975: p. 234) translated Hennig's justification of cladistic methods into the following Popperian "axioms:"

(1) Evolution occurs;
(2) Only one phylogeny of all living and extinct organisms exists, and this phylogeny is the result of genealogical descent;
(3) Characters may be passed from one generation to the next generation, modified or unmodified, through genealogical descent.

These statements contain elements that are necessary for the success of the cladistic method, such as the assumption of a hierarchical pattern. However, the strong assertions of process are sufficient not only to justify Hennig's method, but also to justify methods based on more explicit evolutionary claims, such as ML. Even if we disregard the ontological excess (which is clearly at odds with Popper's goals of minimizing auxiliary hypotheses), Wiley's axioms are too imprecise to provide a demarcation between antithetical approaches and are therefore of limited utility in the cause of cladistics.

Farris *et al.* (1970: pp. 172–174) offered this more abstract set of phylogenetic axioms:

AI A character ("transformation series" of Hennig) is a collection of mutually exclusive states (attributes, features, "characters," "character states," or "stages of expression" of Hennig) which (a) have a fixed order of evolution such that (b) each state is derived directly from just one other state, and (c) there is a unique state from which every other state is eventually derived.

AII For every monophyletic group G, of OTUs, there is at least one character, X, with a state, x, such that if a state y in X describes any OTU in G then (a) y d x,[3] while if a state z in X describes any OTU not in G then (b) z ɖ x.

[3] "d" read "is derivable from," defined by Farris *et al.* to indicate that if one character state is derivable from another, then it is either the same state or apomorphous relative to it.

AIII In the absence of evidence to the contrary, any state corresponding to a step shared by a group, G, of OTUs is taken to have arisen just once in G.

AIV "The more characters certainly interpretable as apomorphous (not characters in general) that there are present in a number of species, the better founded is the assumption that these species form a monophyletic group." (cf. Hennig, 1966: p. 121)

Axiom I mandates that character states be interpreted as nested synapomorphies; axiom II defines monophyletic groups on the basis of this synapomorphy scheme; axiom III restates Hennig's (1966) auxiliary principle, which basically claims that characters provide evidence of grouping; axiom IV says that each character potentially offers independent corroboration of an hypothesis of grouping, implying that character congruence is the measure of clade support. In this view, evolution is invoked in moderation, to justify the ordering of transformations among character states and the elimination of symplesiomorphy as evidence of relationship. By contrast, Platnick (1979: p. 538) identified three principles that he viewed as guiding cladistics. These are

first, that nature is ordered in a single, specifiable pattern which can be represented by a branching diagram or hierarchical classification;
second, that the pattern can be estimated by sampling characters and finding replicated, internested sets of synapomorphies; and
third, that our knowledge of evolutionary history, like our classifications, is derived from the hierarchic pattern thus hypothesized.

This is the much-vilified "pattern cladist" view, which emphasizes that evolution is an explanatory theory for systematic patterns that are observed based on independent theoretical premises (Brady, 1985). See Scotland (1992) for a similar list, again referred to as "axioms of cladistics."

More recently, Kluge (1997) has attempted to describe cladistic hypothesis testing using Popper's (1959) formal axiomatic relationships between hypothesis, evidence, and background knowledge, a problem explored some time ago by Platnick and Gaffney (1977, 1978a,b). In Kluge's scheme, descent with modification is the theoretical background assumption without which cladistic hypotheses cannot be supposed. Kluge (1997: p. 88) repeatedly asserted this in statements such as, "(i)n the case of phylogenetic hypotheses, the assumed background knowledge so critical to testability

is descent with modification (Darwin, 1859: p. 420)."[4] Kluge pooh-poohed pattern cladistics, implying its guilt-by-association with three-taxon analysis (clearly, pattern cladistics and 3TA have nothing to do with one another except that they share some authors, and critique of the latter, no matter how blistering, is irrelevant to the former). In my view, Kluge's Popperian prolixity does not provide a particularly compelling basis for the cladistic approach[5] (nor am I convinced that the procrustean effort to equate particular elements of cladistic analysis variously to *h*, *e*, and *b* is worthwhile). However, the point of this paper is merely to explore the merits of Kluge's claim for the necessity of descent with modification as "the" background assumption of cladistic analysis.

PROCEDURES AND ASSUMPTIONS

The basic sequence of operations in a cladistic investigation is to observe similarities and differences among organisms, formalize these observations as entries in a data matrix, and evaluate the data with an algorithm that infers hierarchically nested sets among the organisms from which the observations were drawn. Some background knowledge is required to justify the raw data, its tabulation into a matrix, the hierarchical pattern, and the grouping algorithm. Farris *et al.* (1970), Wiley (1975), Kluge (1997), and Fitzhugh (personal communication) stated that descent

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[4]It is interesting to contrast those claims with that of Siddall and Kluge (1997: p. 321): ". . . if we discover tomorrow that all life is the product only of special creation, we can still do cladistics, operationally, in terms of summarizing observed character generalities."

[5]For example, clarification of the relationship between logical probability and most parsimonious cladograms implied by the following two apparently contradictory statements would be helpful: ". . . cladists use all of the relevant available synapomorphies, the total evidence, when testing a phylogenetic hypothesis, because a statement describing the results of *multiple* tests (especially if the tests are independent) 'will be less probable than a statement describing only some of the tests' (Popper, 1992: pp. 247–248)—a multiple test result being more improbable, and accordingly *more severe*, than its component tests" (Kluge, 1998: p. 152, italics original) and ". . . the refutationist epistemology of cladistics argues against the use of such a priori weighting, because the assumptions required to justify the expected weights add to background knowledge, which decreases the probability of a cladistic hypothesis in light of its tests" (Kluge, 1998: p. 155).

with modification is a (or "the") necessary element of this background knowledge. Platnick (1979), Brady (1985), and Scotland (1992) stated that it is not, arguing instead that evolution is an explanation for independently inferred cladograms. Is common descent the explanans[6] or the explanandum of cladistics? In the next few paragraphs, I review what I perceive to be the minimal background knowledge necessary and sufficient to perform each of the steps in a systematic investigation, with special consideration for the necessity of a priori evolutionary assumptions.

Observation

An observation is an existential statement that relies on theory. All human knowledge of things in the world is inseparably connected to and mediated by the processes of sensation and cognition (Brady, 1994). Methods of observing, and therefore observations, are judged to be "objective" by the criterion of intersubjective testability, the sophisticated realist approximation to ontological truth (Popper, 1959: p. 44). If everyone agrees that an observation is well-corroborated, then it need not be subjected to additional tests before it can provide plausible background knowledge for subsequent hypotheses (although it *may* be tested if anyone should desire to do so). Such observations can be regarded as "facts" for the next stage of analysis. A good example of empirical systematic data acquired by a generally accepted but theory-laden technique is DNA sequence. Data from methods that are less well-corroborated for various reasons and therefore problematical include morphometric shape characters, DNA–DNA hybridization ΔT_m values, and shared RAPD bands.

The recognition of similarity between features of organisms that provides the basis for conjectures of homology boils down to intersubjective corroboration of observations. That characters are heritable from parents to offspring has been known for thousands of years and provides the basis both for the idea of species and for the idea of their apparent immutability across

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[6]Brady (1985: p. 117) clearly defined "explanans" as the causal explanation of an empirical pattern and "explanandum" as the pattern to be explained. Siddall and Kluge (1997: p. 317 ff.) inexplicably reversed these definitions.

space and time (contra evolution). The striking similarity between certain features of different kinds of organisms has also been recognized for a long time, providing the foundation for comparative biology (e.g., Belon, 1555). To deny that the wing of a bird and the arm of a human are composed of "the same" structures is to deny the observations that have inspired natural philosophers since Aristotle with the notion of a Natural System.

As Hennig (1966: p. 121) recognized in his "auxiliary principle," parsimony is necessary to interpret similar features as evidence of taxonomic grouping, because without that assumption there is no empirical basis for making comparisons between singular phenomena. Sober (1988) discussed a number of complexities in the philosophical justification of common-cause explanations (i.e., parsimony) and suggested that a rationale for assuming common causes should instead be sought proximately, in specific empirical theories. However, as Popper (1979) argued, the "looks-the-same, is-the-same" discrimination rule seems to be a basic cognitive attribute shared among a wide array of animals, providing among other things the basis for the adaptive success of aposematic coloration and mimicry.[7]

Perceived similarities and differences between organisms provide the raw data of cladistics and in my view represent the only necessary ontological foundation for the construction of cladograms and hypotheses of taxonomic grouping. There is clearly an ontological leap between tests of individual observations and tests of "descent with modification," if the latter is even testable without tautology.

Constructing a Data Matrix

Codification of observations into a data matrix has been referred to as the bête noire of systematics (Pogue and Mickevich, 1990). There are alternate ways to carve the features of organisms into characters, alternate ways to divide characters into states, and alternate ways to relate character states to one another (Pleijel, 1995). Differential character weighting and step matrices of character state change may also be employed. Unordered multistate characters with equal weights

may be the least burdened by ad hoc hypotheses and applicable to the broadest range of evidence, thus representing perhaps the closest approach to the parsimony paradigm (Kluge, 1989, 1997), but other approaches have been suggested (e.g., Neff, 1986; Lipscomb, 1992; Goloboff, 1993).

The problems of character coding are complex and may not have a single solution, but the solution or solutions chosen should not depend upon the incorporation of evolutionary background knowledge. One of the major advances of modern systematics is the close attention to exorcising hidden evolutionary assumptions from character descriptions (e.g., a priori designation of polarity). It should be obvious to readers of this journal that the congruence of hypothetically identical character states in cladistic analysis supports the explanatory theory of common ancestry and not the other way around. For cladistic discussions of homology, see Patterson (1982), de Pinna (1991), and Brower and Schawaroch (1996).

Hierarchy

Although it is not in principle demonstrable from external evidence (Panchen, 1992), the existence of a single, irregularly branching hierarchy of relationships among biological taxa has been considered an empirical fact by Brady (1985), based on its historical emergence as the predominant means to represent patterns of taxonomic grouping used by pre-evolutionary systematists during the early 19th century. That this occurred prior to the general acceptance of evolutionary theory by the scientific community is clear evidence that a hierarchical conception of the Natural System is not dependent on an evolutionary process theory (Crow, 1926; Platnick, 1982).

In spite of the occurrence of homoplasy, the irregularly branching hierarchical pattern remains a compelling framework for empirical grouping of taxa based on their similarities and differences and the most natural alternative yet proposed (this argument was offered as early as 1840 by the creationist father of the code of zoological nomenclature, Hugh Strickland). Hierarchy is perhaps best viewed as an epistemological axiom like the principle of parsimony, an unprovable but useful criterion for unambiguously ordering the data (Panchen, 1992), that is divorced from any particular causal hypothesis that might be invoked to explain it.

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[7]It should be noted that the advantage of being a Batesian mimic is based on the potential predator's mistaken inference of homology between convergent features!

de Queiroz and Donoghue (1990: p. 62) criticized this view by arguing that, "(t)he ways that humans represent nature do not necessarily reflect the order inherent in nature, for even artificial classes that do not exhibit nested, hierarchical relationships can be fitted into a hierarchical taxonomy." Their argument is naïve, depending on prior access to metaphysical knowledge of how things in the world truly relate to one another (which is precious limited, even to Harvard men).

From a practical perspective, the "fact" or axiom that an irregularly-branching hierarchy (with or without metaphysical justification) is a useful way of depicting patterns of biological diversity underlies all modern systematic approaches. Like the various methods of observation discussed above, most systematists accept as plausible background knowledge for their studies the assumption that relationships among taxa are productively represented by a hierarchy of groups within groups. Perhaps it is this consensus within the scientific community that has promoted the Natural System's ontological reification as a "real" entity that should be sought in the world.[8] In my view, such concern for the "real" leads to the position that evidence should be suspect because it may not reflect the "true" pattern of phylogeny (e.g., Swofford *et al.*, 1996). Such statements about the condition of things in the world irrespective of evidence may not be tested by scientific inquiry and do not merit further discussion.

Lower Bound of Hierarchy

The problem subject to more ontological interpretations than any other in systematics is the question of species, the least inclusive taxa. The nature of species is a metaphysical quagmire that has been discussed by myriad authors (for some recent debates, see Frost and Kluge, 1994; Baum and Donoghue, 1995; Davis, 1997). Epistemologically speaking, it makes absolutely no difference to systematics what (or if) species "are," as long as some groups of organisms that possess observable features can be recognized as terminals on a branching

hierarchy (Rieppel, 1994; Brower, 1999). The most practical approach is to study exemplar specimens representing the diversity of the particular taxa of interest and to seek among them characters that exhibit hierarchical patterns of variation (Vrana and Wheeler, 1992). It is useful to sample extensively both at hypothetically more and less inclusive hierarchical levels than the level of interest: the former to test monophyly of the ingroup and the latter to test hierarchical structure among terminals (Judd, 1998).

One Optimality Criterion[9]

Although systematists may agree that they are looking for a single hierarchy, they have invented numerous methods by which that pattern may be inferred (cf. Sneath and Sokal, 1973). Interpretations of optimality criteria differ among the various methodological camps, and the choice of method is therefore subject to rather intense debate. However, as Felsenstein (1988: p. 529) noted, "(i)t is unsatisfactory to have several competing approaches if it is not understood how they differ in their assumptions, and thus when one ought to prefer one to another." I would amplify Felsenstein's sentiment to argue that if we believe that the hierarchy of life is usefully represented by a single pattern of groups nested within groups, it is not satisfactory to describe parts of that pattern piecemeal by applying different methods, whether we understand the differences among the methods or not. The principle of parsimony articulated above implies that multiple ways to interpret a single phenomenon are superfluous.

A frequently voiced notion (e.g., Kim, 1993) is that multiple methods of phylogenetic inference should be employed because their agreement on an hypothesis of relationships implies its accuracy. That pluralistic approach is illogical (Farris 1977, 1979a, 1982). There are an infinite number of possible methods that could collectively yield any possible topology. Advocates of the multiple-methods approach (e.g., Bloomer and Crowe, 1998) do not employ most of these possible methods and do not justify their prejudice in choosing the subset that they do employ (perhaps because most possible methods are not available in popular software packages). The current popularity of MP, ML, and NJ

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[8]e.g., Siddall and Kluge, 1997: p. 319: "In phylogenetics, however, we are not interested in some abstract generality regarding the group of taxa we are working with. We are concerned with uncovering the actual spatio-temporally real history of divergence, the species genealogy."

[9]This section should not be construed to advocate any method of phylogenetic inference in particular.

does not justify their exclusive use as "the alternative" methods (if these methods are believed to be "good" because they agree in test cases, then their agreement does not represent much of a test of reliability). To reject some methods and not select one method is arbitrary: if some methods are better than others on principle, then one method is best on the same principle. An analogy to statistical testing is apt: a result may be viewed as significant or not, depending on the choice of statistical methods. Multiple tests of the same data neither provide independent confirmation of a result nor increase our confidence that a result is true. On the other hand, tests that disagree do not together imply that the null hypothesis should be both accepted and rejected. A single, well-chosen method suffices.

The "Natural System" and Cladistics

Throwing away cladistics' evolutionary crutches requires a brief review of the epistemological arguments supporting that method over alternative operationalist approaches, such as phenetic methods. The search for the "true" Natural System of classification of living things has been a metaphysical goal of systematists at least since Linné (1758). By the mid-19th century, philosophers had recognized that certain knowledge of God's Plan of Creation was inaccessible. Epistemological definitions of naturalness were proposed as plausible and operational alternatives to that unattainable systematic nirvana:

> "The ends of scientific classification are best answered when the objects are formed into groups respecting which a greater number of general propositions can be made, and those propositions more important, than could be made respecting any other groups into which the same things could be distributed. . . . A classification thus formed is properly scientific or philosophical, and is commonly called a Natural, in contradiction to a Technical or Artificial, classification or arrangement. The phrase Natural Classification seems most peculiarly appropriate to such arrangements as correspond, in the groups which they form, to the spontaneous tendencies of the mind, by placing together the objects most similar in their general aspect; in opposition to those technical systems which, arranging things according to their agreement in some circumstance arbitrarily selected, often throw into the same groups objects which in the general aggregate of their properties present no resemblance, and into different and remote groups others which have the closest similarity." (Mill, 1843: pp. 466–467)

About a century later, Gilmour (1937: p. 1042) reiterated these ideas. His epistemologically-based notion of a natural classification is "that arrangement of living things which enables the greatest number of inductive statements to be made regarding its constituent groups, and which is therefore the most generally useful for the investigation of living things." "Gilmour naturalness" became the operational goal of phenetic classification in the 1960's (e.g., Sokal and Sneath, 1963), until Farris (1977, 1979a) beat the pheneticists at their own game by demonstrating that cladistic methods produce more "natural" classifications than phenetic methods do. Naturalness, information content, Popperian boldness, simplicity, corroboration, and explanatory power are directly related concepts in systematics, and all are considered to be maximized by the parsimonious arrangement of character state change on Wagner networks (Farris, 1979b, 1982, 1983; Kluge, 1997).

The traditional distinction between phenetic "grouping according to raw similarity" and cladistic "grouping according to putative synapomorphy" (e.g., Farris, 1979b; Sober 1988) implies prior knowledge of character polarity in the cladistic approach, which is usually justified by invoking descent with modification (e.g., Farris, 1986). This would seem to be the major snag for the pattern cladistic rejection of evolution as a part of its background knowledge. However, I believe that a more general description of the cladistic interpretation of character information avoids this problem: a difference between two character states implies a single change and as such can only impart information about a single group.

For example, character 2 in the example matrix (Fig. 1) implies a grouping of either (AB) or (CDE) but not both. Support for a hierarchical structure in cladistics is provided not by the derived or primitive status of character states, but by the parsimonious accounting of transformations between these states. In their calculus of group support, phenetic methods count the same information twice (for example, the "+" group and the "−" group for character 2). Logically incompatible hypotheses of grouping may be implied by the distributions of alternate states in different characters when both states are counted, even if the characters are fully compatible in a cladistic sense, because the complementarity of states of individual characters is contradictory when compared between characters (Farris, 1977). For instance, although this data set implies a single most parsimonious network, the matrix contains
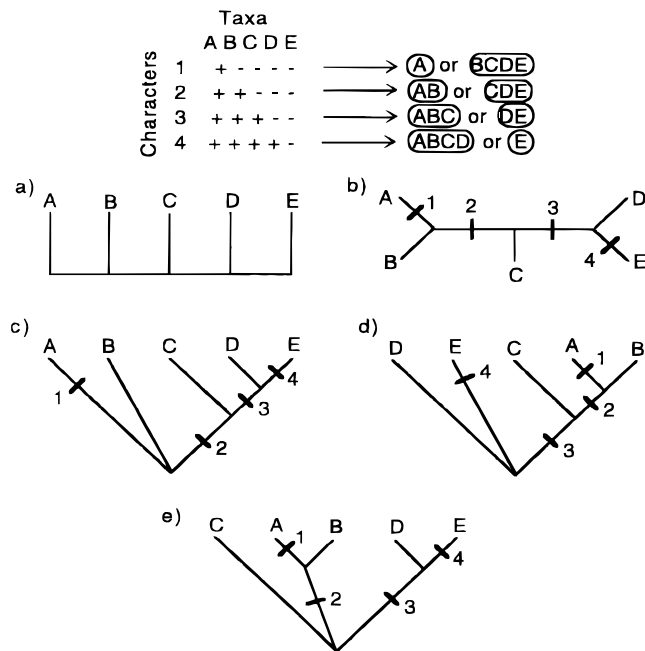
FIG. 1. A data matrix and its implied hypotheses of grouping. Viewing these phenetically (as complementary shared states of incompatible characters) implies the unresolved dendrogram (a). Viewing them cladistically (as character state changes of compatible characters) implies the unrooted cladogram (b) and one of the rooted cladograms (c–e). Polarity information is required to choose a rooted tree.

four pairs of equally "similar" taxa, based on incompatible combinations of shared character states. Grouping of AB is implied by characters 2–4, BC by 1, 3, and 4, CD by 1, 2, and 4, and DE by 1–3. If exclusive groups are defined by the presence of complementary states, then the evidence of grouping implied by each character in this matrix disagrees with the evidence implied by each of the others. This internally contradictory pattern of shared character states employed in phenetic similarity measures accounts for the poor naturalness of phenetic approaches discussed in Farris (1977, 1979a), as well as phenetic problems of taxonomic incongruence due to mosaic evolution (Mickevich and Johnson, 1976; Mickevich, 1978).

A criticism here might be that "evolution" and "modification" in their most basic sense are synonymous with "change," as descriptive terms. However unlike some recent authors (e.g., Patterson, 1994; Siebert and Williams, 1998), I see no necessary connection between the notion of transformation as a relation that unites the states of one character with respect to those of other

characters and any particular material cause. Farris (1980: p. 391) made a similar point: "It might seem that the accuracy of the transformational interpretation depends on that of the phylogenetic hypothesis. As an historical theory, it does indeed, but as a description of the observed character, it is correct whether the postulated phylogeny is right or not." It is the ontological connotation of evolution in the context of biological systematics, and not the word "transformation" itself, which is objectionable (Brady, 1994).

Character Polarity and Rooting

It hardly needs to be reiterated that in standard cladistic analysis, the length of most parsimonious cladograms is unaffected by the position of the root (Farris, 1970), that current programs build unrooted networks, and that a priori character polarization is therefore unnecessary (Farris *et al.*, 1970). Yet the historical distinction between cladistics and phenetics, and many of the prior axiomatizations of cladistics (see above), implies that apomorphy must be recognized before groups can be recognized and that therefore an unrooted cladogram is at best an incomplete hypothesis or at worst is evidentially vacuous. Such a characterization is simply inappropriate: many hypotheses of relationship are rejected by parsimonious selection of the shortest unrooted cladograms, and only the distinction of monophyly versus paraphyly of groups remains to be determined by locating the root (Lundberg, 1972). Indeed, as taxa are added to the analysis, the position of the root accounts for a diminishing proportion of possible topologies (see Appendix). If the discovery of the most parsimonious tree is the essence of cladistics, then I would argue that unrooted cladograms approach the ultimate goal of cladistic analysis, because rooting (which implies the directionality of character state change) occurs after tree inference. This point would seem to recommend the standard approach over three-taxon analysis (for current debate, see Siebert and Williams, 1998; Farris and Kluge, 1998; de Laet and Smets, 1998), since the latter's dependence on a priori character polarization can be viewed as an undesirable auxiliary hypothesis.

A posteriori rooting can be based on either ontogenetic criteria (Nelson, 1978; de Pinna, 1994) or outgroups (reviewed in Nixon and Carpenter, 1993). Regardless of whether one or the other of these is

generally superior, neither requires evolutionary background knowledge. The order of appearance of features in ontogeny is empirically observable, and it has been employed as a criterion for inferring branching patterns since pre-evolutionary times (von Baer, 1828; Barry, 1837). Outgroup rooting is based only on the easily testable hypothesis that the taxa of the ingroup are a clade with respect to a particular outgroup. There is quite good intersubjective agreement on the monophyly of many groups, and where there is not, the tree may be represented as partially unrooted. A rooted tree is just a representation of a hypothetically distal part of a larger (or the single) hierarchy. In any event, if the ingroup is connected by more than one branch to the other taxa represented in an unrooted cladogram, the hypothesis of ingroup monophyly is rejected (Brower, 1999).

To summarize this section, the axioms I consider necessary and sufficient for cladistics are:

1. Observed character differences among taxa provide the evidentiary basis;
2. An irregular bifurcating hierarchy is a useful way to represent relationships among taxa; and
3. Parsimony is the guiding epistemological principle of the systematic endeavor.

I have tried to show that these three rules (one ontological, two and three epistemological) logically entail all the other criteria, such as grouping by synapomorphy, that are frequently invoked as a priori axioms of cladistics (cf. Farris *et al.*, 1970; Scotland, 1992). "Pattern cladistics" is thus a tenable position, but is it better than "process cladistics"?

PATTERN CLADISTICS REDUX

Much of Hennig's ontological justification of phylogenetic systematics was feeble, for two reasons. First, the bearing of the "facts" (the processes of ontogeny and tokogeny) he asserted to support the existence of the process of phylogeny that in turn accounted for the hierarchical pattern of taxonomic groups is a metaphorical extrapolation from observed short-term to unobserved long-term processes. Even if that argument

were plausible, an a priori phylogenetic rationale would pave the way for the admission of rampant ad hoc systematic argumentation based on evolutionary phenomena "beyond the immediately observable" (Baum and Donoghue, 1995), including the models of character state change required by ML methods. Second, it is difficult to imagine what empirical pattern might be proscribed by a more general assumption of evolutionary background knowledge, such as "descent with modification," as invoked by Kluge (1997) and others. Descent explains pattern similarity, modification explains pattern difference, and their combination can explain any pattern that might be observed. Popper (1959: p. 92; 1974: p. 136) viewed such notions as metaphysical and unfalsifiable, which clearly renders them undesirable as background auxiliary hypotheses.

Although Willi Hennig's influence on the subsequent development of systematics cannot be overestimated, it is necessary to discard metaphysical Hennigian baggage when it no longer serves the interests of the discipline. The assumption of evolution in process cladistics is a methodological plesiomorphy (Carpenter, 1987) that no longer contributes to the discovery of hierarchical patterns of taxonomic grouping. Nowhere in the procedures described above, which are those used by cladists of every stripe today, is an evolutionary assumption required in general or particular.

The process of phylogeny that explains the hierarchical patterns discovered by systematics is one of the most profound empirical theories of modern science. I have not claimed that macroevolution is poorly corroborated and therefore not intersubjectively plausible (macroevolution is one of my personal favorite theories, and I teach my undergraduate students that it is "true"). Instead, my argument is that the theory of macroevolution is corroborated by evidence from systematics (i.e., comparative anatomy, paleontology, biogeography, and more, recently, comparative biochemistry). Therefore, the a priori assumption of descent with modification fails to provide independent ontological support for systematics. If "the background knowledge of descent with modification" underlying cladistics is not testable by independent means, it would seem to be more a metaphysical First Principle like vitalism or orthogenesis than a component of a Popperian hypothetico-deductive approach.

Even if a testable assumption of evolution were sufficient to justify a subsidiary and derivative systematics, the discussion above shows that it is unnecessary. Because evolution-based systematics relies on supernumerary assumptions, it has lower explanatory power than and is philosophically inferior to pattern cladistics. Siddall and Kluge (1997) have criticized the ML approach with the argument that it is a basic logical fallacy to justify a method with a theory that is derived directly or indirectly from the results of that method, and Kluge (1997: p. 91) has stressed that, "(a)dding to background knowledge is a verificationist slippery slope, which ultimately leads to tautology." It is thus alarming to find these authors proclaiming that their process cladistics is predicated upon the same ontological slippery slope that the advocates of ML have enthusiastically descended.

Although pattern cladistics should hold a strong appeal to those who see parsimony as the guiding principle of the systematic endeavor, the recent literature is pocked with attacks against that perspective from a variety of recidivist philosophical camps (e.g., de Queiroz and Gauthier, 1990; Baum and Donoghue, 1995). Kluge and various coauthors have argued from a diversity of such positions over the past few years in this very journal. To wit, when discussing total evidence, Kluge and Wolf (1993) advocated abduction to the best explanation as an alternative to hypothesis testing in a Popperian framework. In their investigation of the nature of species, Frost and Kluge (1994) adopted a similar abductivist point of view against the hypothetico-deductivist view of taxa as universal statements (essential classes; see Popper, 1959; Kitts and Kitts, 1979) and argued that "operationalism can be the result of failure to appreciate that consilience of inductions marks progress in science" (p. 286). On the other hand, refutationist hypothetico-deductivism underlain by "the background knowledge of descent with modification" was wielded against "verificationist" views (including consilience) in Kluge (1997), while "sophisticated falsificationism" is used to the same ends in Siddall and Kluge (1997). Philosophy is central to the advance of theoretical systematics, but when inconsistently invoked as a weapon of convenience, the label of "mumbo jumbo" may indeed be apt. Bewildering one's opponents with kaleidoscopic tirades of philosophical arcana is an intimidating rhetorical device, but the rhetoric is ultimately self-defeating if there is no coherent and defensible basis for the ideas espoused. Cladists can do better.

APPENDIX

The number of unrooted bifurcating topologies is equal to

$$\frac{(2t - 3)!}{2^{(t-2)}(t - 2)!},$$

where t is the number of terminal taxa (Edwards and Cavalli-Sforza, 1964; Fitch and Margoliash, 1968). For any one of these trees, the number of possible positions of the root is equal to $2t - 3$. Adding one taxon increases the number of unrooted topologies by $2(t + 1) - 3$, but the number of possible positions of the root on any one of these by only 2. Therefore, as t increases, the position of the root becomes a smaller and smaller factor in determining the hierarchical pattern of grouping among the taxa.

A simpler way to envision this is to consider two adjacent (or "neighboring" sensu Lundberg, 1972) terminals on an unrooted network of t taxa. There are $2t - 3$ branches in the network, and only placing the root on one of the two branches leading to the two terminals will imply that they are not sister taxa, a ratio of

$$\frac{2}{2t - 3}.$$

Obviously, as t increases, the chances that neighboring taxa in an unrooted cladogram will not be sister taxa in the rooted cladogram decreases. Although the argument is more complicated for internal nodes connecting larger adjacent parts of an unrooted network, the basic idea still holds.

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