Parsimony with and without Scientific Justification

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Brower's (2000, *Cladistics* 16, 143–154) pursuit of a nonevolutionary cladistics, like those of others (e.g., Scotland, 2000, *Syst. Biol.* 49, 480–500), fails for lack of a scientific justification. His operational explication of parsimony does not necessarily rule out the use of other criteria on which to base the identification of a hierarchical branching pattern, nor does he give a compelling reason for why just that one kind of pattern is sought. In the absence of evolutionary theory, such as the descent of species, and the modification of character states, one from another, there is no scientific reason to seek congruence among character hierarchies whose origins, functions, and fates are not necessarily the same. Brower's operational parsimony is no substitute for phylogenetic parsimony, where requirements for *ad hoc* hypotheses of homoplasy are justifiably minimized, assuming only "descent, with modification." In addition to maximizing explanatory power, that most parsimonious cladogram is the least disconfirmed, most highly corroborated, hypothesis.   © 2001 The Willi Hennig Society

INTRODUCTION

Brower (2000, p. 143) states that evolution is a sufficient assumption in the inference of phylogeny, as proposed by Kluge (1997, 1998a, 1999), but he argues that no premise of evolution is really necessary in seeking a hierarchical pattern of relationships. Brower explores some, but not all, of the consequences of presupposing evolutionary principles, such as "descent, with modification" (Darwin, 1859). For example, he does not touch on the fact that a hierarchical pattern could have any number of kinds of explanation, of which one might be evolutionary relationships. Or, that pattern might have no explanation at all. By that I mean "have no *scientific* explanation," where explanation is achieved by deducing effect from cause, in light of an explaining law or general theory, during the inference of the hierarchical pattern. To better understand these particular possibilities, I review the nature of scientific explanation and Farris' (1983; see also Kluge, 1997) and Brower's (2000) arguments for parsimony, which I refer to as "phylogenetic parsimony" and "operational parsimony," respectively. The research programs to which phylogenetic and operational parsimony belong have been called phylogenetic systematics and pattern cladistics, respectively. I follow Brower's use of the term "pattern cladistics" for his approach, while recognizing that his axiomatization is not exactly like that of others who have called themselves, or been labeled, pattern cladists (e.g., Platnick, 1979; Scotland, 1992, 2000). I begin with a brief consideration of *rational* justification, because that is what must accompany a *scientific* choice of methods, including that of parsimony.[1]

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[1]Sober's (1975) lengthy discussion of the concept of simplicity covers many of the points I make concerning a justification for parsimony in phylogenetic inference.

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JUSTIFICATION

Empirical scientists claim their research leads to increased knowledge, through explanation, and such progress appears to be true in most cases. It seems equally fair to say, however, that few researchers actually attempt to *justify* their inferential methods and results in just that way. Nonetheless, Hume (1739) long ago recognized the importance of justification, arguing that knowledge must be distinguished from belief and concluding that knowledge is belief based on rational justification (Sober, 1988, p. 42).

The nature and importance of rational justification can be illustrated with a simple example of enumerative induction, which lacks a rational justification (from Salmon, 1966). Assume a number of balls are removed from an urn, and all of the black ones in the sample are found to taste like licorice. What rational justification can be given to the inference that the black balls remaining in the container taste like licorice? More generally, what justifies enumerative inductive inference, from the repeatedly observed to the unobserved? This kind of question remains without a compelling answer, and enumerative induction has yet to be successfully justified (Siddall and Kluge, 1997). Scientists cannot be content with an inference scheme just because it provides a result that "seems to make sense." For results to be more than an article of faith (an empty hierarchical construct, in the case of pattern cladistics), the operationalism responsible for the results must be rationally justified. To be able to claim *why* the operationalism "seems to work" requires justification.

SCIENTIFIC EXPLANATION

Scientific explanations must meet two criteria, that of relevance and testability. With respect to relevance, the explanatory information brought forward must provide a sound basis for believing the phenomenon to be explained did, or does, occur. A hypothesis that is relevant is also testable, although the opposite is not always true. Scientific explanation occurs when the elements in a hypothesis are connected to the causal mechanism(s) responsible for a phenomenon. Scientific explanations are distinctly causal.

One of the standards used in developing a fuller understanding of explanation is the covering-law model of Hempel and Oppenheim (1948; see also Popper, 1959), which was formulated originally according to a deductive scheme of inference. In this model, one or more explaining laws or general theories (L_1, L_2, L_3, ..., L_n) and a set of sentences describing the appropriate initial circumstances (C_1, C_2, C_3, ..., C_k) are taken as premises and constitute the *explanans* when conjoined, which provides a sufficient, or nearly sufficient, condition for the event E, the *explanandum*, which is to be explained. Summarizing,

L_n: explaining law(s) or general theory(s)

C_k: specific initial conditions(s) (cause)

_____   explanation

E: specific event (effect) .

It was with this kind of formalism that I explored the explanatory nature of phylogenetic systematics (Kluge, 1999), where Darwin's (1859) principles of "descent, with modification" were assumed as the explaining theories (L_{1-2}), with the cladogram, and its common ancestral relations, constituting the specific initial condition (C_1), and synapomorphy the specific event to be explained (E). Summarizing:

L_{1-2}: "descent, with modification"

C_1: cladogram

_____   explanation

E: synapomorphy .

Defining the concept of homology as "features (parts, attributes) that were present in the common ancestor in which they are homologous" (Ghiselin, 1984) provided the inheritance model of explanation that is attributed to Farris (1983).[2] Summarizing:

L_{1-2}: "descent, with modification"

C_1: cladogram

_____   explanation of inheritance

E: synapomorphy as homology .

[2]Brower (2000, p. 146) asks: "Is common descent the explanans or the explanandum of cladistics?" I believe it is neither, if the explanation is one of inheritance (*sensu* Farris, 1983). In that model, the *explanans* is "descent, with modification, *plus* the cladogram, while the *explanandum* is synapomorphy as homology.

From my reading of *On the Origin of Species* (Darwin, 1859, pp. 430–431; see also pp. 123–124, 333, 340–341), the "descent" principle means that species evolve from other species, as opposed to species being created independent of one another, and the "with modification" principle means that the traits of species are transformations of prior states (e.g., $c \rightarrow t$, thymine substituted for cytosine), as opposed to abstract, timeless, relations of character states (e.g., $c–t$). Moreover, I agree with Popper (1957, pp. 106–107; 1980; 1984) that both of these Darwinian principles are testable (Kluge, 1999). Of course, testability is evident only when cladograms are understood as phylogenetic hypotheses, and shared-derived character states constitute potentially disconfirming evidence (see also Kluge, 1999, pp. 430, 434).

Brower (2000), on the other hand, takes a different position on the meaning and testability of Darwin's most general principles. He asserts (Brower, 2000, p. 151) that

> [d]escent explains pattern similarity, modification explains pattern difference, and their combination can explain any pattern that might be observed.

Thus, I would argue that it is only Brower's misreading of Darwin's principles that has led him to conclude that "descent" and "with modification" are

> metaphysical and unfalsifiable, [and] which clearly renders them undesirable as background auxiliary hypotheses.

It is Brower's *unjustified* hierarchical pattern that is in fact an unscientific metaphysical construct. It is untestable.

PHYLOGENETIC PARSIMONY

Parsimony has long played a prominent role in science as a methodological injunction in the evaluation of competing hypotheses, and its use in phylogenetic inference has been no less distinguished (Kluge, 1984). Unfortunately, the question of what is minimized in a phylogenetic proposition has not always been made clear by those who employ the rule of parsimony, and that shortcoming seems to have contributed to the "aura of determinism and certainty" imagined by some of parsimony's most outspoken critics (e.g.,

Felsenstein, 1983a, p. 322). Brower's (2000) paper is an example of one that advocates parsimony, but fails in its justification.

In phylogenetic inference, a most parsimonious hypothesis is understood to either minimize ad hocisms or postulate fewer natural processes. In the discussion to follow, the term phylogenetic parsimony is employed for what constitutes ad hocism (Farris, 1983), "plausibility parsimony" for the minimization of some natural process(es). These uses are equivalent to Kluge's (1984, p. 26) "methodological" and "evolutionary" types of parsimony, respectively. In addition, there is operational parsimony (see below).

The distinction between phylogenetic and plausibility parsimony has been understood for many years (Kluge, 1984). Early papers that clearly emphasize the minimization of *ad hoc* hypotheses include those by Hennig (1950, 1966), Wagner (1961, 1980), Kluge and Farris (1969), and Farris *et al.* (1970). In fact, minimizing *ad hoc* hypotheses was the cornerstone of Farris' (1983) classic *The Logical Basis of Phylogenetic Analysis* (see also Farris and Kluge, 1986, 1997).

Among the earliest papers that appeal to a process model justification of parsimony in phylogenetic inference, such as assuming *a priori*, if only implicitly, that change is improbable, were Edwards and Cavalli-Sforza (1963, 1964), Camin and Sokal (1965), Eck and Dayhoff (1966), Fitch (1971), and Felsenstein (1973a,b, 1979). In fact, it was Edwards and Cavalli-Sforza (1963, p. 553) who precisely defined plausibility parsimony:

> The most *plausible* estimate of the evolutionary tree is that which invokes the minimumnett [sic] amount of evolution [my italics].

A more fully developed likelihood justification for plausibility parsimony is contained in Sober's (1988, p. 212) "Smith–Quackdoodle" Theorem. In this, a hypothesis of homology is considered more plausible than a separate cause of homoplasy when the independent origin of the synapomorphous states is relatively unlikely. For example, arguing by analogy from family names, Sober claimed a greater likelihood of common ancestry (a common causal explanation) for two persons sampled at random from the U.S. population who happened to be named Quackdoodle, relative to finding two that were named Smith.

Unfortunately, in addition to oversights by operationalists, such as Brower, the distinction between phylogenetic and plausibility parsimony is almost always

overlooked by verificationist phylogeneticists (e.g., Felsenstein, 1983a,b, 1993; Sober, 1988; see however Sober, 1993; Swofford *et al.*, 1996; Steel and Penny, 2000) or denied altogether (e.g., Edwards, 1996; see review by Farris and Kluge, 1997). For example, Bull *et al.* (1993, pp. 386–387) were correct when they claimed that

> [t]he *model* of evolutionary process is explicit in maximum-likelihood reconstruction, whereas it is largely implicit in other methods such as parsimony . . . [my italics],

but only if the parsimony they had in mind was plausibility parsimony. Brower (2000, p. 144) then compounds their error in failing to make the distinction between phylogenetic and plausibility parsimony when citing Bull *et al.*, and others who hold positions similar to theirs, and that is because he looks at parsimony operationally rather than normatively. His disdain for philosophy results in this error. Future debates over phylogenetic inference methods would certainly benefit from distinguishing falsificationism from verificationism, including phylogenetic parsimony from plausibility parsimony. Making other distinctions, such as background knowledge arguments versus model conditionals, would no doubt help as well (Siddall and Kluge, 1997).

The criterion of parsimony has long been identified with algorithms that search for the shortest length cladogram, i.e., for species relationships that minimize character state transformations (number of steps) (e.g., Kluge and Farris, 1969). However, it was not until 1983 that Farris made abundantly clear that the reason for employing parsimony in phylogenetic systematics is the minimization of requirements for *ad hoc* hypotheses of *homoplasy* (reversal, convergence, and parallelism). Not *ad hoc* hypotheses of any kind, but *ad hoc* hypotheses of homoplasy! Unfortunately, this logic of phylogenetic parsimony is rarely mentioned any more. For example, nowhere does Brower (2000) relate parsimony to the minimization of *ad hoc* hypotheses in the special sense of Farris (1983; see also Steel and Penny, 2000, p. 839).

The problem with *ad hoc* hypotheses is that they have no relevant and/or decisive test implication. *Ad hoc* hypotheses are usually introduced *a posteriori* into a discussion for the sole purpose of saving a cherished hypothesis from the threat of disconfirming evidence

or theoretical inconsistency. Such hypotheses are simply appeals to authority, which are incapable of being critically examined. As Farris (1983, p. 17) succinctly argued, *ad hoc* propositions are to be avoided, because

> [s]cience requires that choice among theories be decided by evidence, and the effect of an ad hoc hypothesis is precisely to dispose of an observation that otherwise would provide evidence against a theory. If such disposals were allowed freely, there could be no effective connection between theory and observation, and the concept of evidence would be meaningless.

The special problem with an *ad hoc* hypothesis of homoplasy is that it is an *ad libitum* explanation, one capable of explaining patterns and nonpatterns alike, and in being able to do so, it explains nothing at all. In addition, there is the problem that homoplasy is just error (Kluge, 1999). These are the basic arguments that justify the use of parsimony in phylogenetic systematics.

Character transformations are merely counted in operationalizing phylogenetic parsimony; the precise probabilities of change are not evaluated. This is the standard, unweighted, form of parsimony, where all characters are analyzed simultaneously and no particular significance is attached to the weight of any particular step (or the total weighted length of a cladogram) (Kluge, 1998a). Assuming no common mechanism, beyond the processes of "descent, with modification," the phylogenetic hypothesis of greatest likelihood is equivalent to the least disconfirmed, most parsimonious, cladogram (Theorem 5 of Tuffley and Steel, 1997, p. 599; Steel and Penny, 2000). And, it is in this sense, even though prior probabilities are not included, that a least disconfirmed, most parsimonious, cladogram can be maximally corroborated and of greatest likelihood (Farris *et al.*, 2001). It may also be said that such a hypothesis maximizes explanatory power, more synapomorphies being explainable as due to inheritance, from a common ancestral condition, owing to the minimization of requirements for *ad hoc* hypotheses of homoplasy (Farris, 1983; Kluge, 1999).

OPERATIONAL PARSIMONY

Brower states (2000, pp. 143, 151) that three nonevolutionary axioms are together necessary and sufficient for generating what he calls an "irregular hierarchical

pattern of relationships": (1) "the discoverability of characters"; "[o]bserved character differences among taxa provide the evidentiary basis;" (2) "hierarchy"; "[a]n irregular bifurcating hierarchy is a useful way to represent relationships among taxa;" and (3) "parsimony"; "[p]arsimony is the guiding epistemological principle of the systematic endeavor." He goes on to say (p. 146) that

> [t]he basic sequence of operations . . . 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.

And, the payoff, according to Brower (see also e.g., Platnick, 1979; Brady, 1983, 1985; Nelson and Platnick, 1981, 1991; Nelson, 1989; Scotland, 1992, 2000), is that the resulting pattern can then be used as *independent evidence* for evolution. However, this leaves unanswered how a hierarchical pattern can be interpreted as evidence for evolution when the algorithm imposes the hierarchical pattern to begin with. It is not as if there is any other option besides hierarchy. So (Brower, 2000, p. 146), what is the

> background knowledge [sic] [that] is required to justify the raw data, its tabulation into a matrix, the hierarchical pattern, and the grouping algorithm[?]

My principal focus in this paper is on Brower's justifications for grouping, i.e., his arguments for operational parsimony.

Brower's (2000) justification for operational parsimony amounts to four kinds of arguments: (1) The philosophy of operationalism (for which Brower uses the term epistemology), where the goal is to maintain a logical gap between theory and evidence (Hull, 1968); (2) The idea that knowledge of phylogeny has been, and must continue to be, derived from classifications based on nonevolutionary methods; (3) If evolutionary theory is to be testable with cladograms, it cannot be assumed in the inference of phylogeny. (4) What is presumed to be wrong with plausibility parsimony constitutes an argument for operational parsimony.

While my review to follow is not exhaustive of each of those kinds of arguments, it does illustrate the scope of Bower's attempts to justify operational parsimony, which is critical to his pattern cladistics. Unfortunately, Brower's statements often contain more than one of the aforementioned four kinds of argument, which has

kept me from organizing their discussion into just those four categories. It also follows that there is some redundancy in my review and for which I apologize to the reader.

(a) Page 144: Brower states that

> [p]arsimony is an epistemological approach . . . that restricts the realm of inferential reasoning to interpretation of evidence in the *simplest theoretical framework* necessary and sufficient to *account* for the data [my italics; see Sober, 1975].

However, Brower does not explain the nature of that *theoretical framework* in which the simplest accounting is to be understood. If *simplest account* is taken to mean that some form of process explanation is minimized, which is a kind of plausibility parsimony, this does not rule out evolutionary theory as necessary to a theoretical framework, such as provided by a deductive form of inference. Indeed, without knowing what the theoretical framework is, one cannot be sure that a simple accounting is any more appropriate than a complex one. The nature of simplicity in the context of the theoretical framework of Popperian testability is taken up immediately below.

(b) Pages 144–145: Quoting Popper (1959, p. 82), Brower claims that

> [e]xtra background assumptions should be discarded, because they weaken the capacity of the empirical evidence to discriminate among competing theories.

And elsewhere he states (p. 152) that

> [b]ecause evolution-based systematics relies on supernumerary assumptions, it has lower explanatory power than and is philosophically inferior to pattern cladistics.

Brower's point is that operational parsimony is justified, because it makes no background assumptions, whereas phylogenetic parsimony cannot be justified that well, because it assumes "descent, with modification." This leaves unanswered what guiding theory is used to collect data, and, presuming that there must be one, the results of an analysis of those data cannot be theory-free.

Further, the full text of Popper's (1959) thoughts on background assumptions indicate Brower's misunderstanding of deductive inference and the role that background knowledge assumptions play in it. For example, Popper argued (pp. 82–83) that

> [a]s regards auxiliary hypotheses we propose to lay down the rule that only those are acceptable whose introduction does

not diminish the degree of falsifiability or testability of the system in question, *but, on the contrary increases it* [my italics].

In other words, Popper's system of testability requires sufficient background knowledge to be able to identify a test statement and from which an explanation might be claimed. According to the covering law model of explanation,

L_n: explaining law(s) or general theory(s)

C_k: specific initial condition(s) (cause)

———————————————————————— explanation

E: specific event (effect) ,

I assert that Brower's pattern cladistics does not offer explanation, nor can it claim to maximize explanatory power, in the absence of an explaining law or general theory, such as provided to phylogenetic parsimony by "descent, with modification."

Moreover, falsifiability cannot be what Brower (2000, p. 146) has in mind when he speaks of reviewing

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.

Indeed, there is no testability in his axiomatization of pattern cladistics,

the discoverability of characters, hierarchy, and parsimony.

In fact, given just these three axioms, there is reason to believe that the

single, irregularly branching hierarchy of relationships

sought by Brower (2000, p. 147) is arrived at by enumerative induction, merely the congruence of character patterns, and not deductively with critical evidence (Farris *et al.*, 2001).

Other misunderstandings are suggested (Kluge, 1997, pp. 84–85), since Brower confuses minimizing background knowledge with *ad hoc* hypotheses in his argument for operational parsimony. No part of Popperian testability, either degree of corroboration, **C(h,e,b)**, or severity of test, **S(e,h,b)**, directly references *ad hoc* hypotheses (Popper, 1963, p. 288). As Farris (1995; p. 115) pointed out, that

[*a*]*d hoc* hypotheses do have low corroboration

does not make them part of the logical probability of Popper. Further, phylogenetic parsimony, with its logic in minimizing requirements for *ad hoc* hypotheses of homoplasy, has nothing to do with the argument for *simplicity* in testability. As Popper (1972, p. 81; 1983, p. 225) made clear, the extent of the content of hypothesis **h** is a function of the *simplicity* and clarity with which **h** can be described, and the higher the content of **h**, the bolder **h**. And, as I had emphasized (Kluge, 1997, p. 85), simplicity and explanatory power are directly related by virtue of their formal relationship to logical probability, and while the number of *ad hoc* hypothesis is also connected to explanatory power, that relationship is complementary. Accordingly, the least disconfirmed, most highly corroborated, cladogram is identified with phylogenetic parsimony, which minimizes requirements for *ad hoc* hypotheses of homoplasy and thereby maximizes explanatory power (Kluge, 1997; Farris *et al.*, 2001). To be sure, the auxiliary assumptions that constitute background knowledge are kept to a minimum, but they must be sufficient to justify a test statement, where **h** is defined as simply and as clearly as possible. Those conditions of **h** are met in the enumerated possible cladograms that are to be tested. As Siddall and Kluge (1997) emphasized, all possible completely bifurcating hypotheses of sister species relationships are logically determined by the number of terminal taxa in the data matrix. This is a closed set of hypotheses, and it is the testing of these alternatives that is the focus of phylogenetic systematics. In principle, identifying the most parsimonious, fully resolved cladogram has nothing to do with its "generation" (*contra* Brower).

(c) Page 145 (see also 143): Brower[3] argues that

. . . the strong assertions of process [Wiley's (1975, p. 234) "descent, with modification"] are sufficient not only to justify Hennig's method, but also to justify methods based on more explicit evolutionary claims, such as ML [maximum-likelihood].

This is simply incorrect, because maximum-likelihood, like all plausibility parsimony methods, requires model assumptions, in addition to the auxiliary, background knowledge, assumptions of "descent, with modification" (Siddall and Kluge, 1997).

(d) Page. 145: According to Brower, Hennig's (1966) auxiliary principle

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[3]Throughout, Brower does not distinguish evolutionary pattern theory, "descent, with modification," from evolutionary process theory, such as a constant rate of evolution.

basically claims that characters provide evidence of grouping.

However, Hennig intended more in his principle. As he (p. 121) stated,

> the presence of apomorphous characters in different species 'is always reason for suspecting kinship . . . , and that their origin by convergence should not be assumed a priori . . . '[P]hylogenetic systematics would lose all the ground on which it stands' if the presence of apomorphous characters in different species were considered first of all as convergences (or parallelisms), with proof to the contrary required in each case.

And, axiomatically,

> [i]*n the absence of evidence to the contrary,* any state corresponding to a step shared by a group G, of OTUs is taken to have arise just once in G [this is axiom III of Farris *et al.*, 1970, p. 74; my italics].

Thus, what Brower leaves out is the scientific basis on which homology can be distinguished from homoplasy.

(e) Page 145: According to Brower,

> . . . axiom IV [of Farris *et al.* (1970)] says that each character potentially offers *independent* corroboration of an hypothesis of grouping, *implying* that character congruence is the measure of clade support [my italics].

Aside from seeming to conflate corroboration with congruence, this is a misinterpretation of Farris *et al.*'s (p. 174) axiom IV:

> 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.

Axiom IV emphasizes the distinction between apomorphy ("derived steps"; p. 175) and plesiomorphy (character states in general), not independence among characters. Further, while axiom IV may imply congruence, that axiom by itself is not sufficient to distinguish phylogenetic parsimony from a method like clique analysis, the former leading to a most parsimonious hypothesis, in which all of the evidence is integrated, both congruent and incongruent synapomorphies, the latter leading to a branching pattern that explains only the largest set of unique and unreversed synapomorphies. The distinction between phylogenetic parsimony and clique analysis is clear when compared in terms of explanatory power; the former maximizes that power, whereas the latter does not necessarily do so. Brower's operational parsimony provides no basis for distinguishing between those methods, which opens the door to asking: Why operational parsimony? Why not clique analysis?

(f) Page 147: Brower is content to argue that

> 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.

Useful perhaps, but there is no argument in this for why parsimony is *necessary,* there being other methods, such as compatibility and Prim network analyses, for making comparisons between singular phenomena (see below). The importance of phylogenetic parsimony lies in its explanatory power, in its minimization of requirements for *ad hoc* hypotheses of homoplasy for all of the available evidence, *thereby* maximizing those novelties explainable as homologues and so providing evidence of taxonomic groups. Again, without a justification, there is no compelling reason to choose operational parsimony over any other method of grouping, such as clique analysis.

(g) Page 147: Brower appeals to the cognitive skills of animals (including those of systematists),

> looks-the-same, is-the-same . . .,

as sufficient to pick out congruent characters. This argument is naive. Consider the now well-founded unparsimonious nature of nucleotide characters, where an intentionally defined state (adenine, cytosine, guanine, or thymine) at a nucleotide site is nonetheless incongruent, which means that "is-the-same physicochemically," "is not the same in a group relation context."

(h) Page 147: When Brower argues that

> [u]nordered multistate characters with equal weights may be the least burdened by *ad hoc hypotheses* . . . [and the] closest approach to the parsimony paradigm (Kluge, 1989, 1997) [my italics]

he confuses *a priori*, auxiliary, assumptions with *a posteriori*, *ad hoc*, assumptions. The auxiliary class of assumptions includes background knowledge and model assumptions. The distinction between background auxiliary assumptions and *ad hoc* hypotheses has already been discussed above. When Brower uses the term *ad hoc* hypothesis it always seems to be in reference to auxiliary assumptions and as such has no relationship to Farris's (1983) justification for phylogenetic parsimony,

the minimization of requirements for ad hoc hypotheses of homoplasy.

(i) Page 147: Brower's statement, that

[i]t should be obvious to the readers of this journal that the congruence of hypothetically identical character states in cladistic analysis supports the explanatory theory of common ancestry . . .,

overlooks the fact that conjoining even the true phylogeny with congruent synapomorphies does not *by itself* lead to a deduction of homology, because those two assumptions do not rule out the possibility of parallelism (Kluge, 1999, his Fig. 1). An additional assumption of evolutionary process, in addition to "descent, with modification," is required to cover all cases of inference of synapomorphous states being inherited from the same common ancestral condition, i.e., being homologous (Farris, 1983). The verificationist strategy is to estimate independent evolution (including parallelism) probabilistically, but in order to do that some sort of model must be assumed. This model is what characterizes plausibility parsimony (e.g., the Smith–Quackdoodle theorem, the abductive likelihood assumption of Sober, 1988). Operational parsimony eschews all process assumptions, which leaves unanswered the questions: What constitutes the evidence for monophyletic groups? What justifies the recognition of homologues? Phylogenetic parsimony simply declines to rule on the hypothesis of parallelism by minimizing *ad hoc* hypotheses of homoplasy.

(j) Pages 147–148: Brower treats both hierarchy and parsimony as epistemological axioms, as "unprovable but useful" criteria for "unambiguously ordering the data," as "divorced from any particular causal hypotheses that might be invoked to explain" them. But, why seek a *single* most parsimonious hierarchical pattern? Observations are made on the parts of organisms, such as the DNA, tissues, organs, physiology, and behavior. These represent a variety of different scalar hierarchies, each with its own origin, function, and fate (Frost and Kluge, 1994). As such, each kind of character data used in a pattern cladistic analysis can have a different pattern. Indeed, each character of each kind of data can have its own pattern. Consider, for example, different gene trees. Thus, it cannot be judged "an empirical fact" (*contra* Brady, 1985), as Brower (2000, p. 147) claims, that there exists

a single, irregularly branching hierarchy of relationships among biological taxa . . .

Brower's (2000, p. 148) assertion is wrong that

[e]pistemologically 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 . . .

To the contrary, without a concept species, there is no compelling reason to believe the state relations of different characters should conform to a single hierarchical pattern, as delivered by operational parsimony (Frost and Kluge, 1994). Further, without a concept species, males and females might be coded as different terminals. That the parsimony algorithm seeks, and often finds, a single most parsimonious branching pattern is merely a consequence of the chosen operationalism. The parsimony criterion itself does not necessarily provide any special insight into the relationship between pattern and process.

Without premises as to what a most parsimonious hierarchy is intended to explain, and be a test of, we are left to take the axioms of "hierarchy" and "parsimony" on faith. Scientists require more than the claims

that an irregularly-branching hierarchy . . . is a *useful* way of depicting patterns of biological diversity . . .,
that relationships among taxa are *productively* represented by a hierarchy of groups within groups . . .,

and especially so when the subjectivisms "useful" and "productively" go undefined. That *all* systematists might even agree that hierarchy is to be assumed is no more a scientific argument than is believing the last black ball to be sampled from an urn will taste like licorice, just because all previously sampled black balls tasted like licorice. Rational justifications are required for both conclusions. Descriptive generalizations are of two basic kinds, universal and historical, and identifying the kind of pattern, which may not be hierarchical (e.g., the Periodic Table), requires a general theory that can be rationally justified as part of an *explanans* (Hull, 1974; Kluge, 1999, p. 410).

(k) Pages 148–149: Brower argues that parsimony is the preferred optimality criterion for generating a single hierarchical pattern of relationships, because

it is not *satisfactory* to describe parts of that pattern piecemeal by applying different methods . . . [my italics].
The principle of [operational] parsimony articulated above implies that multiple ways to interpret a single phenomenon are *superfluous* [my italics].

A single, *well-chosen* method suffices [my italics].

Even accepting, as I do, Farris' (1977, 1979, 1982) position that methodological pluralism is illogical, the question of "why parsimony" at all requires an answer. For phylogenetic parsimony, the answer is clear; see Farris (1983). For operational parsimony, the answer is a matter of faith: it works.

(l) Page 149: Brower asserts that

[n]aturalness, information content, Popperian boldness, simplicity, corroboration, and explanatory power are directly related concepts in systematics, and all are considered maximized by the parsimonious arrangement of character state change on Wagner *networks* . . . [my italics].

There is much to disagree with in this statement. For example, the nonevolutionary "Natural Classification" of Mill (1843, pp. 466–467; see also Gilmour, 1937, p. 1042), in which Brower sees virtue (see also p. 147), concerns intentionally defined class concepts and their induction (such as "snub-nosed humans" and the Periodic Table). That kind of Natural Classification has nothing to do with the results of "descent, with modification," historical events, and their deduction. There is no argument here for operational parsimony, if its results are to be used in *testing* evolution. Necessarily unique events are not to be confused with class concepts (Popper, 1957).

Also, as discussed above, the concepts of Popperian boldness and simplicity, and their operational definitions, have nothing to do with being maximized by the parsimonious arrangement of character state relations. And still further, that Wagner networks are the same length as their rooted equivalents does not mean that a network has explanatory power (*sensu* Farris, 1983). A network is not characterized by "time's arrow," the relation that allows Hennig's (1966) special similarity to be explained as inheritance, from a common ancestral condition. The usefulness of forming networks in heuristic parsimony algorithms is not to be confused with what is ultimately to be explained. There is after all the distinction between plesiomorphy and apomorphy, and those relations are interpreted on a directed, phylogenetic hypothesis of relationships. And furthermore, we are left to wonder why Brower's nonevolutionary operationalism leads to a preference for Wagner networks, instead of Prim networks, the former with, and the latter without, hypothetical internodes. After all, Prim networks have been proven

to be a most efficient, cost-effective kind of pattern for connecting telephone terminals (Prim, 1957).

(m) Pages 149–150: Brower claims that

[s]upport 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 [my italics].

But, what does transformation mean, if not change from one state into another? This is nothing more than prevaricating on the subject of evolution. Even counting steps (transformations) parsimoniously we are still left to contemplate why the parsimony method is employed and what is meant by synapomorphy, if not shared-*derived* character states. Brower's explanation for how support is achieved, without evoking the concepts of "descent, wit modification," is hardly compelling—he just *sees*

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. It is the ontological connotation of evolution in the context of biological systematics, and not the word 'transformation' itself, which is objectionable . . .

At the very least, this amounts to an argument that is not independent of merely assuming abstract, timeless relations (**c–t**) among the features of organisms, and we are left to ask: What is it that constrains Brower to certain character state relations? What is it that defines different characters?

(n) Page 150:

If the discovery of the most parsimonious tree is the essence of cladistics, then [Brower] 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.

In making this argument for operational parsimony Brower is still faced with having to employ what he calls "a posteriori rooting," rooting the network according to ontogenetic criteria or outgroup/ingroup hypotheses. Their use, however, is burdened with one or more assumptions, and the savings in assumptions in a posteriori rooting Brower leaves unargued.

(o) Page 151: And finally, Brower summarizes his position with the claim that

[t]he 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.

This bold statement, however, amounts to nothing more than supposing a history of phylogenetic systematics that has yet to occur, while ignoring the significant role that evolution has played in shaping our current practice of cladistics. For example, "descent, with modification" was critical in challenging the tradition of differential character weighting, including *a priori*, implied, and *a posteriori* weighting (Kluge, 1998b).

SUMMARY

According to Brower (2000; p. 145; see also p. 143), pattern cladistics (Platnick's, 1979, and Scotland's, 1992, 2000, versions, as well as his own) leads to

> systematic patterns that are observed based on independent theoretical premises [the axiomatizations of Platnick, Scotland, and Brower],

and for which

> evolution is an explanatory theory . . .

So, pattern cladistic analysis seeks an *undefined* kind of "irregular branching pattern" with a parsimony algorithm, which is *then* explainable in evolutionary terms, such as "descent, with modification." What is wrong with this picture? The crux of the problem is the absence of rational justification. For example:

Problem 1: What justifies grouping taxa together, if it is not their sharing one or more apomorphic states? Brower argues that his assumption of transformation is not evolutionary, because it does not specify a time-ordered relation among the states of a character. However, to claim groups are identifiable in such a network space only begs the question. Without a causal explanation, such as involving "descent, with modification," synapomorphy is not interpretable as homology.

Those taxic pattern cladists who deny transformation at all (e.g., Scotland) fare even worse. As Kluge and Farris (1999, p. 207) pointed out,

> [t]he taxic choice of ((A B) (C D)) . . . rests on ruling out *a priori* the possibility that either state [of a binary character, $(A B)_0$ (C D)$_1$] has replaced (changed into, been substituted for) the other. If applied to nucleotide data, then, the taxic assumption would have the paradoxical implication that substitution could not have occurred at all!

I say their position is worse, because it is not just

neutral with respect to evolutionary theory, but antagonistic to it.

Problem 2: What justifies a hierarchical branching pattern? If pattern cladistics is to have no metaphysical bias, as Brower claims, then there is no reason to be limited to just that kind of pattern (*contra* Scotland, 2000, p. 498). Without searching for it, how is one to know that the pattern is not of some other form, a circular array, a reticulate pattern, a periodic order? The Periodic Table has certainly demonstrated its predictiveness. Why not the nodeless Prim network? Such networks have certainly demonstrated their cost-effectiveness.

Problem 3: What justifies the exclusive use of parsimony? Why not use some other criterion for seeking the singular branching pattern? As Brady (1994, p. 19) contended,

> . . . any scheme that produces a good fit with the data is worthy of consideration . . .

Indeed, compatibility analysis identifies one branching pattern on which the largest number of characters analyzed are congruent and for which there is an evolutionary explanation, that of being unique and unreversed. That pattern is most parsimonious, and its explanation is even consistent with "descent, with modification"!

Problem 4: Why must the hierarchy be so parsimoniously constructed as to require hypothetical internodes. Why not Wagner or Prim networks?

Problem 5: Why seek just one, most parsimonious branching pattern? Without assuming a theory up front, like species genealogy (Darwin's "descent" principle of evolution), there is no justification for being constrained to just one the number of patterns observed among the characteristics of organisms (Frost and Kluge, 1994). Thus, it must be taken on faith that the branching pattern produced by operational parsimony provides independent evidence of "descent, with modification."

The payoff in Brower's version of pattern cladistics is illusory, given the failure of his arguments for operational parsimony (see also Scotland, 2000). Further, while Brower embraces testability (e.g., 148), the branching pattern obtained from operational parsimony seems to be the result of enumerative induction. One need only to have read Woodger (1937) to see that axiomatization in biology means nothing without

explanation and testability (e.g., Popper, 1959, pp. 71–72). Since operational parsimony and pattern cladism more generally have yet to receive a rational justification, they must be considered unscientific. Achieving

a logically independent theory of systematics . . .,

as Brower claims to have accomplished, is of no real interest to cladists, whose primary concern is knowledge of the empirical world of which species are a part.

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