Kuhnian Values and Cladistic Parsimony

Richard Richards
University of Alabama

According to Kuhn, theory choice is not governed by algorithms, but by values, which influence yet do not determine theory choice. Cladistic hypotheses, however, seem to be evaluated relative to a parsimony algorithm, which asserts that the best phylogenetic hypothesis is the one that requires the fewest character changes. While this seems to be an unequivocal evaluative rule, it is not. The application of the parsimony principle is ultimately indeterminate because the choice and individuation of characters that figure in parsimony computations are indeterminate. The cladistic approach is Kuhnian because the application of parsimony depends on persuasion, background, training and tradition.

1. Introduction

Thomas Kuhn, in his essay "Objectivity, Value Judgment and Theory Choice,"[1] recalls a conclusion that he had arrived at in his *Structure of Scientific Revolutions* fifteen years earlier.

> I considered the ways scientists are brought to abandon one time-honored theory or paradigm in favor of another. Such decision problems, I wrote, "cannot be resolved by proof." To discuss their mechanism is, therefore, to talk "about techniques of persuasion, or about argument and counterargument in a situation where there can be no proof" (Kuhn 1977, p. 320).

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1. This essay, published in *The Essential Tension* (1977), was based on a lecture delivered in 1973 at Furman University.

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For Kuhn, theory choice cannot be "resolved by proof" because there is no unequivocal algorithm or rule of theory choice. He makes this clear in a similar discussion presented in his 1969 postscript to the second edition of the *Structure of Scientific Revolutions.*

> Debates over theory-choice cannot be cast in a form that fully resembles logical or mathematical proof. In the latter, premises and rules of inference are stipulated from the start. If there is disagreement about conclusions, the parties to the ensuing debate can retrace their steps one by one, checking each against prior stipulation. At the end of the process one or the other must concede that he has made a mistake, violated a previously accepted rule. After that concession he has no recourse and his opponent's proof is then compelling (Kuhn 1970, p. 199).

He concludes:

> There is no neutral algorithm for theory-choice, no systematic decision procedure which, properly applied, must lead each individual in the group to the same decision (Kuhn 1970, p. 200).

Theory choice, according to Kuhn, is instead made by reference to a set of scientific *values,* which influence but do not determine theory choice.

According to Kuhn, simplicity is one of these values. This is hardly surprising. Simplicity—or parsimony[2]—has long been regarded as a value. William of Ockham, a fourteenth century scholastic, is often credited for valuing parsimony in his counsels that "multiplicity is not to be assumed without necessity," and that "what can be done with fewer is done in vain with more." In agreement with these counsels, parsimony is usually taken to be a criterion of theory choice: given a set of otherwise equal hypotheses, the simplest, most parsimonious hypothesis is the best hypothesis, and consequently should be preferred over less parsimonious hypotheses. But, as Kuhn argues, values like simplicity are not rules or algorithms. They cannot be applied unequivocally because first, different values may conflict; and second, an individual value like parsimony may be interpreted and applied in different ways.

This indeterminacy in the application of values choice does not initially seem to square with the recent, systematic application of a parsimony rule

2. I will not be distinguishing simplicity and parsimony here, although it is possible to do so. Elliott Sober, for instance, identifies simplicity with inductive generalization, and parsimony with causal reasoning (Sober 1991, p. 50). The concerns I will be raising here apply equally to both simplicity and parsimony in Sober's sense.

in "cladistics"—the now predominant approach to inferring the evolutionary past.[3] Cladistic theory choice is based on a parsimony principle, which asserts that the best phylogenetic hypothesis is the hypothesis that requires the fewest assumptions of evolutionary change. Based on this principle, phylogenetic hypothesis evaluation seems to be merely a matter of following the parsimony rule—counting the evolutionary changes required by each hypothesis, ranking the hypotheses according to relative parsimony, and adopting the most parsimonious of the hypotheses. It seems that here Kuhn's account fails: cladistic hypothesis choice is no more indeterminate than simple addition, and can therefore function as an algorithm or rule of theory choice.

The cladistic parsimony principle has not gone unchallenged, but the scrutiny has almost exclusively focused on its justification: does cladistic parsimony presuppose that nature, or evolutionary change, is parsimonious in some way?[4] While there is no consensus on this issue,[5] the cladistic approach has remained attractive because it apparently presents an unequivocal rule of hypothesis choice.[6] Whether or not cladistic parsimony can really function this way, will be my focus here.

I will be arguing that, contrary to appearances, cladistic parsimony is in fact a Kuhnian value, because its application is ultimately indeterminate in the ways Kuhn describes. The source of this indeterminacy is to be found in the fact that evolutionary change—the quantity minimized by cladistic parsimony—is typically understood in terms of changes in character states. The number of evolutionary changes required by an hypothesis is therefore a consequence of the number of characters that change.

3. This approach became known as cladistics because of its emphasis on cladogenesis, the branching associated with speciation. Cladistics is based on a set of methodological prescriptions advocated by the East German entomologist Willi Hennig in the 1950s and 1960s. The main competing approach is 'evolutionary systematics.' See Hull (1988). See also Mayr (1981).

4. Cladists generally deny that there is such a presupposition. Gaffney, for instance, credits Ockham, for recognizing the value of parsimony, then claims that parsimony might be considered "a methodological rule," and accepted "not because it mirrors reality in some way" (Gaffney 1979, p. 98). Sober (1988) argues against Gaffney and others, that cladistic parsimony relies on some assumptions about nature, but not always the same assumption.

5. D. J. L. Quicke, in his textbook discusses this issue, then argues: "Attempts to justify parsimony have not been successful, but neither have attempts to show that it is fatally flawed" (Quicke 1991, p. xii).

6. Philippe Janvier argues this explicitly: "The use of *parsimony* as a criterion for preferring one hypothesis of phylogenetic relationship to another makes the chosen hypothesis accessible to *refutation* or *falsification*" (Janvier 1984, p. 47). And "Cladistics provides rules, based on logic, and a comparative biologist who rejects these rules can be compared with a chemist who rejects Mendeleev's periodic table . . . " (Janvier 1984, p. 56).

Consequently, the relative parsimony of a phylogenetic hypothesis is influenced by character individuation. But there is no single, generally accepted principle of character individuation, which instead *seems* to be a consequence of social factors like disciplinary traditions, pedagogical context and persuasion. This suggests that the application of cladistic parsimony in hypothesis choice can favor different hypotheses depending on the social factors that influence character individuation. The recognition of this influence encourages a closer look at Kuhn's suggestion, in the passage quoted above, that to explain theory choice we need to refer to "techniques of persuasion." This suggestion has been controversial, leading to criticisms that theory choice for Kuhn is just a matter of "mob psychology," and that choice is therefore not based on good reasons (Lakatos 1970, p. 178; Scheffler 1967, p. 81).

To make my case that cladistic parsimony is a Kuhnian value, I will explain first, Kuhn's account of values and the source of indeterminacy in their application; second, the application of cladistic parsimony and how it initially seems to provide an unequivocal rule of theory choice; and third, the indeterminacy of character individuation and how it renders the application of the parsimony principle indeterminate. I will follow that with a brief sketch of how character individuation engages Kuhn's claim that theory choice is best accomplished on the basis of persuasion and group decisions.

2. Kuhnian Values

In the essay quoted at the beginning of this paper, Kuhn denies that there is an unequivocal rule or algorithm of theory choice. In this same essay, he also denies that theory choice is therefore unguided.

> . . . I sketched in my closing chapter a number of characteristics that scientists share by virtue of the training which licenses their membership in one or another community of specialists. In the absence of criteria able to dictate the choice of each individual, I argued, we do well to trust the collective judgment of scientists trained in this way. "What better criterion could there be," I asked rhetorically, "than the decision of the scientific group?" (Kuhn 1977, p. 320).

This explanation of theory choice in terms of group decision, led to charges of mob psychology by his critics, which Kuhn lamented.

> My views, it is said, make of theory choice "a matter of mob psychology." Kuhn believes, I am told, that "the decision of a scientific

> group to adopt a new paradigm cannot be based on good reasons of any kind, factual or otherwise" (Kuhn 1977, p. 321).

To clear up this perceived misunderstanding arising from his earlier book, Kuhn explains how scientific groups arrive at decisions about theory choice. Rather than rules or algorithms of theory choice, scientific groups employ *values* in theory choice. Kuhn identifies five: accuracy, consistency, breadth, simplicity, and fruitfulness (Kuhn 1977, pp. 321–322). What is important for Kuhn is that these values influence rather than dictate theory choice (Kuhn 1970, p. 199). They are like the more familiar, everyday values—quality of life, freedom of speech, and preservation of life and property—which similarly influence without determining choice of action.

These values cannot function as algorithms of theory choice because, first, there are multiple values, and values often conflict. Accuracy may favor one hypothesis while simplicity or scope may favor another (Kuhn 1977, p. 322). And because there is no single rule to unequivocally resolve conflicts among values, in cases of conflict, theory choice is ultimately indeterminate. Second, as Kuhn explains, the application of each individual value is itself indeterminate. This is in part because a value may be interpreted in more than one way. As we may disagree about what constitutes speech in our protection of free speech, we may also disagree about what constitutes breadth, simplicity, or scope.[7]

Given such indeterminacy, it is easy to see how individual scientists might come to apply values differently. But if the best criterion of theory choice is the decision of a scientific group, as Kuhn argues, the individuals comprising the group must also be able to achieve some sort of consensus.[8] This is accomplished, according to Kuhn, through *persuasion.*

> To understand why science develops as it does, one need not unravel the details of biography and personality that lead each individual to a particular choice, though that topic has vast fascination. What one must understand, however, is the manner in which a particular

7. Kuhn claims that Copernicus' model of the heavens is simpler than Ptolemy's model—if simplicity is interpreted in terms of "mathematical apparatus." But if simplicity were instead to be interpreted in terms of "computational labor," Copernicus' system offered no advantage (Kuhn 1977, p. 334).

8. I don't find the notion of a 'group decision' to be very clear. One concern is that most decisions are primarily individual decisions, and that consensus is merely arriving at the same decision—not by some action of a group. We can all individually agree, for instance that $2 + 3 = 5$, without ever doing anything *as a group.* It doesn't seem to me however, that Kuhn requires that these decisions all be the product of group actions in the stronger sense.

> set of shared values interacts with the particular experiences shared by a community of specialists to ensure that most members of the group will ultimately find one set of arguments rather than another decisive. That process is persuasion . . . (Kuhn 1970, p. 200).

A full analysis of Kuhn's views about persuasion is beyond the scope of this paper, but a brief sketch can give us an idea of what he has in mind. For Kuhn, persuasion is not verbal in the usual sense.

> Two men who perceive the same situation differently but nevertheless employ the same vocabulary in its discussion must be using words differently. They speak, that is, from what I have called incommensurable viewpoints. How can they even hope to talk together much less to be persuasive[?] (Kuhn 1970, p. 200).[9]

Instead, persuasion, when successful, results in the adoption of a new viewpoint.

> To persuade someone is, I take it, to convince him that one's own view is superior and ought therefore supplant his own (Kuhn 1970, p. 203).

Kuhn explains that what partly constitutes the adoption of a new viewpoint, is a new grouping of objects on the basis of similarity. This grouping is accomplished by reference to "exemplars."

> The practice of normal science depends on the ability, acquired from exemplars, to group objects and situations into similarity sets which are primitive in the sense that the grouping is done without an answer to the question, "Similar with respect to what?" One central aspect of any revolution is, then, that some of the similarity relations change. Objects that were grouped in the same set before are grouped in different ones afterward, and vice versa. Think of the sun, moon, Mars and earth before and after Copernicus; of free fall, pendular and planetary motion before and after Galileo; or of salts, alloys and sulphur-iron filing mix before and after Dalton (Kuhn 1970, p. 200).

Kuhn describes exemplars as "shared examples of successful practices" (Kuhn 1977, p. 318), "standard examples" (Kuhn 1977, p. 306), and as "concrete problem solutions accepted by the group as, in a quite usual sense, paradigmatic" (Kuhn 1977, pp. xix, 229, and 298). The inclined

9. The suggestion is that if two people occupy two different viewpoints, they can use the same words but mean different things. This incommensurability thesis is far too complex for me to say much of value here.

plane, the conical pendulum, and Kepler's ellipses are exemplars for solving motion problems (Kuhn 1977, p. 306). And individual ducks, swans and geese in the park are exemplars for solving taxonomic problems (Kuhn 1977, p. 313). According to Kuhn, learning how to solve new problems is accomplished by learning to see how they are like standard examples (Kuhn 1977, p. 305).

Since I shall be returning to Kuhn's conception of exemplars later in this paper, and with a particular application in mind, I will set discussion of exemplars aside, except to note the following. First, exemplars are of fundamental importance to Kuhn. In fact, he tell us that the original meaning of 'paradigm', was as exemplar.

> It is, of course, the sense of "paradigm" as standard example that led originally to my choice of that term. Unfortunately, most readers of *The Structure of Scientific Revolutions* have missed what was for me its central function and use 'paradigm' in a sense close to that for which I now suggest "disciplinary matrix" (Kuhn 1977, p. 307).

Second, since the similarity sets and their associated viewpoint are accepted on the basis of exemplars, persuasion must consist partly in convincing others to adopt a particular exemplar. So, insofar as persuasion guides group decisions about the application of values, theory choice is at least partly based on exemplar choice.

I will in the remainder of this paper be applying Kuhn's account of theory choice to the application of parsimony in cladistic phylogenetic inference. But in order to do this, I must say something about the application of cladistic parsimony.

3. Cladistic Parsimony

Simplicity is one of the values identified by Kuhn as functioning in theory choice. Phylogeneticist E. O. Wiley identifies parsimony with simplicity, then advocates it as a criterion of theory choice.

> Two or more hypotheses frequently compete against each other in explaining the same data. In such a case, the principle of simplicity (parsimony) is used to pick the hypothesis that explains the data in the most economical manner . . . For our purposes in phylogenetics the most parsimonious or simplest hypothesis is that with the fewest ad hoc statements that explains the full array of available data (Wiley 1981, p. 20).

Eldredge and Cracraft argue similarly:

> . . . Science must formulate a criterion by which to judge the relative merits of our close approximations (hypotheses). That criterion, in effect, is parsimony, and it specifies the most preferred hypothesis . . . " (Eldredge and Cracraft 1980, p. 67).

Randall Schuh, in a recent textbook, similarly advocates a parsimony criterion, as an optimization criterion that bases hypothesis choice on minimizing the assumptions of evolutionary change. Schuh then describes it as an algorithm of hypothesis choice.

> In cladistic analysis optimization involves minimizing the number of character-state changes—ad hoc hypotheses—on a cladogram. As such, optimization is the application of parsimony to the establishment of phylogenetic relationships. Choice or rejection of a hypothesis is determined by the fit of the data to the hypothesis, that is, by the number of independent character originations required on a cladogram . . . Optimization methods are *algorithms,* a series of steps in a process, that ultimately allow for determination of which hypotheses best describe the data under a given criterion (Schuh 2000, p. 116).

In general, the cladistic parsimony principle is understood to assert that the best phylogenetic hypothesis is the hypothesis that requires the fewest assumptions of evolutionary changes.[10]

The phylogenetic hypotheses to be evaluated in terms of parsimony are typically hypotheses of *sister groupings*—the grouping of each taxon with the most closely related taxa.[11] Typically, sister groupings are represented by cladograms in terms of branching order. In the following cladogram (Eldredge and Cracraft 1980, p. 51), a. indicates the hypothesis (AB)C—the taxa (species, genera, etc.) A and B are sister groups, because they have a more recent common ancestor—as represented by the branching order. In b. A and C are sister groups excluding B, while in c., B and C are sister groups.

10. Schuh suggests that the assumed changes are independent. It is not obvious either what this means, or that cladists in fact use only independent character originations in parsimony computations. Similar formulations can be found in Minelli (1993, p. 34), Janvier (1984, p. 55), and Farris in Humphreys and Funk (1984, p. 330).

11. Phylogeneticists may also be concerned with ancestor-descendent relationships (are birds descended from dinosaurs?), but they are most concerned with sister grouping, or in cladistic terms, placing taxa in monophyletic groups, where each group or taxon contains all and only the descendent species of a single ancestral species. Because monophyly is the basis of biological taxonomy and represents real phylogenetic relations among taxa, it is important to get this sister grouping right.

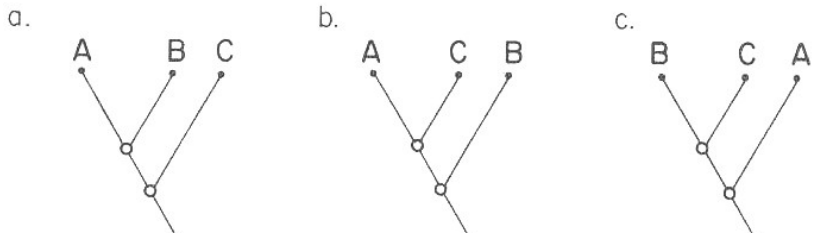

Figure 1

Cladograms like these are generated on the basis of shared characters—similarities. We infer that two species have recent common ancestry because they are *similar* in some way. Robins and sparrows, for instance, are similar because they diverged relatively recently from a common ancestor. But not all similarities indicate common ancestry, some indicate analogous adaptive responses. Marsupial wolves and placental wolves, for instance, are believed to be similar because of analogous adaptive change to similar environments. One basic task of phylogenetic inference then, is to distinguish the similarities that indicate common ancestry (homology) from those that do not (homoplasy).

The cladistic approach does this through a simple injunction: *assume* homology. This is an application of the parsimony principle, because homology requires one change in a single common ancestral species, while homoplasy requires two changes in independent lineages. We can see how parsimony works in the following cladogram from Eldredge and Cracraft (1980, p. 25). Eldredge and Cracraft describe how they might generate this cladogram using a parsimony principle. Given a group of taxa, the first step is to note the similarities and differences.

> The problem at hand is to construct a cladogram for the following organisms: cat, mouse, lizard, perch, and lamprey . . . The first task is to undertake a survey of the anatomy of these organisms and to note the similarities and differences. This morphological comparison indicates that the five organisms exhibit a broad structural diversity . . . how are the observed similarities among the five organisms to be evaluated so that a cladogram may be constructed? (Eldredge and Cracraft 1980, p. 22).

Then, according to this method, we assume that each of the similarities is an homology (originating in a single common ancestor) and group the taxa according to the possession of these similarities. The first grouping

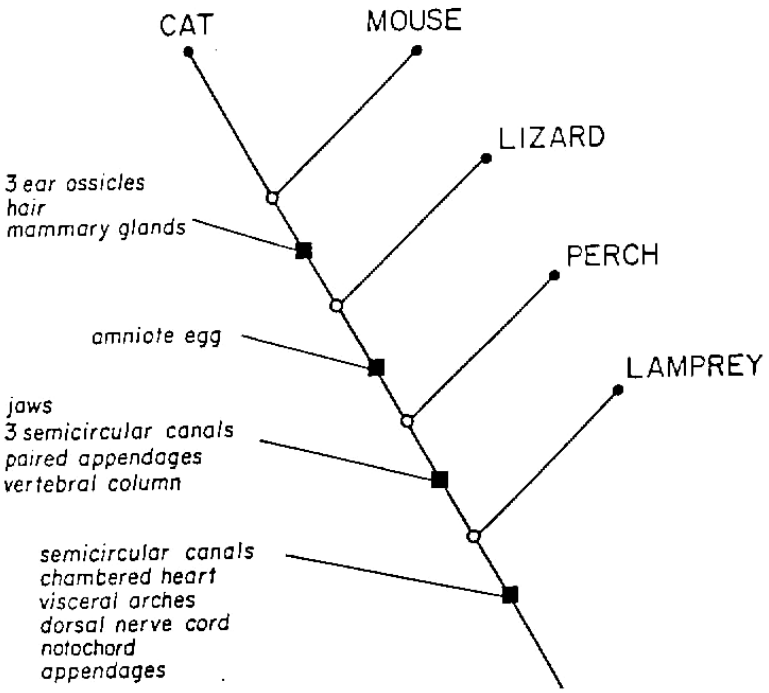

Figure 2

will be based on those similarities that all the organisms share (ancestral homologies or symplesiomorphies).

> The first question to be asked then, is: What are the general similarities shared among the organisms that could be used to define a group containing all five (termed the *universal set* of the comparison)? There happen to be a number of these similarities: semicircular canals in the head, a chambered heart, visceral (gill) arches at one or more stages of the life cycle, a dorsal nerve cord, a notochord, and appendages of some kind (Eldredge and Cracraft 1980, p. 23).

Any other similarity, if it is not found in all five taxa, will identify some subgroup of that universal set.

> . . . Similarities such as amniote egg indicate a set comprised of lizard, cat, and mouse. On the other hand, the perch resembles the

> lamprey in having a non-amniote egg, and thus might be grouped with the latter; and the lizard, perch, and lamprey have neither hair nor mammary glands implying they might comprise a subgroup (Eldredge and Cracraft 1980, p. 23).

These similarities that identify subgroups are evolutionary novelties or "derived homologies" (synapomorphies). For cat and mouse in this cladogram, "3-ear ossicles," "mammary glands," and "hair" are derived homologies, and identify these taxa as constituting a subgroup.[12]

In generating this cladogram, Eldredge and Cracraft are assuming, as enjoined by the parsimony principle, that the characters identified (ear ossicles, hair, amniote egg, etc.) are each homologies, indicating a single evolutionary change in an ancestral species. If any of these characters were homoplasies, had independent origins in different taxa, additional changes would be required.

Eldredge and Cracraft (1980, p. 68) explain this application of parsimony relative to three taxa *A, B,* and *C,* and a single character a, where a′ indicates a change in character state (see figure 3). In a., the hypothesis *(AB)C,* which indicates that *A* and *B* have a more recent common ancestor than either have with *C* (A and B are therefore a sister group), implies a minimum of one change in character state (represented by the solid bar), because a′, the derived stated, originated once in the ancestor of *A* and *B.* In b. and c., there are a minimum of 2 changes each, one in *A* and one in *B* (as homoplasies). Parsimony therefore requires that we choose the hypothesis *(AB)C,* and reject *(AC)B* and *(BC)A.* Here, it seems, the parsimony principle, applied to a single character, is an unambiguous rule of hypothesis choice.

In the cladogram containing cat, mouse, lizard, etc., the parsimony principle is applied without conflict; the most parsimonious hypothesis relative to each character is consistent with the most parsimonious hypotheses relative to other characters. But more typically, the most parsimonious hypothesis for one character is not the most parsimonious for other characters. This conflict in applying the parsimony principle to each character can also be resolved by parsimony, whereby some similarities assumed to be homologies based on parsimony, get reinterpreted as homoplasies instead. Eldredge and Cracraft illustrate how this works in figure 4. In d-f, we can see the conflict: the hypothesis *(AB)C* is most parsimonious for the characters a′, b′, d′, and f′ , while *(AC)B* is most parsi-

12. The idea is that there will be at least one character associated with the appearance of new taxa. The key to sister grouping therefore lies in the identification of the derived homologies that can identify the sister groups.

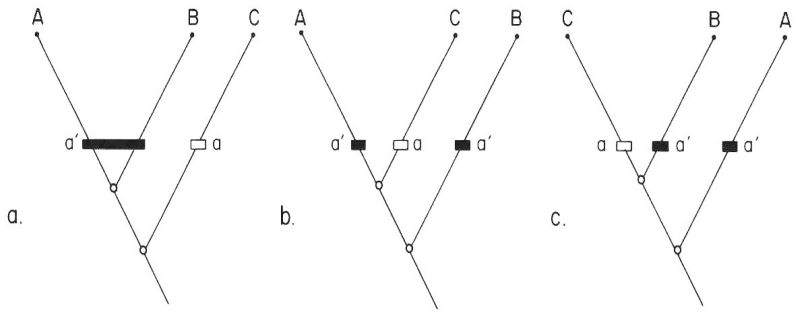

Figure 3

monious for c′ and e′. If, however, we reinterpret the conflicting homologies as homoplasies, then in d., phylogenetic hypothesis *(AB)C* is favored by four derived homologies (long bars) a′b′d′ and f′, implying four changes, but is opposed by two, c′ and e′, which must be reinterpreted as homoplasies, implying four more changes, for a total of eight changes. In e., *(AC)B,* there are two derived homologies (two changes) but four homoplasies (eight changes) for a total minimum change of 10. In f., *(CB)A,* all six characters must be homoplasies, indicating a minimum of 12 total changes. Of these three possible phylogenetic hypotheses then, *(AB)C* is the most parsimonious (8 minimum changes), followed by *(AC)B* (10 minimum changes) and *(BC)A,* 12 minimum changes. Parsimony therefore provides an unequivocal ranking of hypotheses, with *(AB)C* as the best or most preferred hypothesis, followed in order by *(AC)B* and *(BC)A.*

4. Character Sets

Given a particular set of characters, as I have described in the simple examples above, cladistic parsimony might plausibly be regarded as an unequivocal rule of hypothesis choice. There are, however, several sources of indeterminacy. First, the application of cladistic parsimony is indeterminate—even relative to a single data set—because there are different parsimony algorithms, based on the sorts of changes allowed. J. Felsenstein explains:

> The parsimony or minimum-evolution approach has been the source of several alternative methods, in which different combinations of evolutionary events are allowed to occur and the numbers of different types of inferred character-state changes are to be minimized. These include the Wagner parsimony method . . . the Dollo

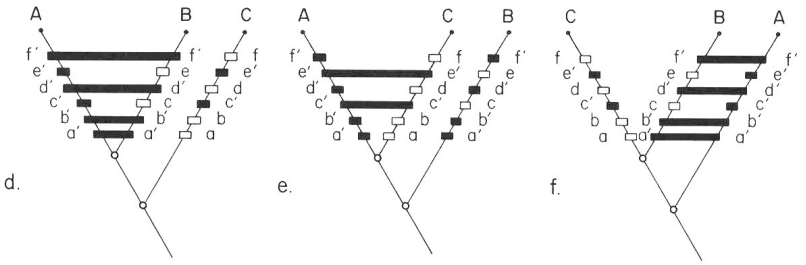

Figure 4

> parsimony method . . . and the polymorphism parsimony method . . . (Felsenstein 1984, p. 171).

Other algorithms include the "Camin-Sokal Method" and "Non Additive Fitch Optimization." Significantly, the parsimony ranking of hypotheses varies according to which algorithm is used (Schuh 2000, p. 117).

The details of the application of each of these algorithms are beyond the scope of this paper, but it is significant that cladistic parsimony can be applied in different ways—even if we assume that it is evolutionary changes that are minimized. The mere adoption of the parsimony value does not tell us which algorithm to use. This squares well with Kuhn's claim that values like simplicity can be interpreted in different ways by different individuals, and therefore be unable to unequivocally determine theory choice.

Second, it should also be apparent that parsimony considerations depend on the formulation of the data set—which characters count in parsimony consideration. Phylogeneticists are aware of that fact. Duncan and Stuessy, for instance, emphasize the importance of the formulation of the character set:

> Selection of characters and character states is the most important part of a cladistic analysis . . . Reconstructions of the branching sequences of phylogeny and whatever classifications may be derived from it are entirely dependent on the careful and skillful treatment of the characters and states (Duncan and Stuessy 1985, p. 50).

But as will become apparent, it is doubtful that the selection of characters for the data set can be accomplished by anything like a rule or algorithm. Because of this, the application of parsimony cannot be unequivocal. While I cannot do justice to the complexity of specific problems confronting phylogeneticists here, a brief sketch of some of the main considerations will illustrate this indeterminacy.

In the simple example above, the parsimony rule was applied to characters like 'amniote egg', 'hairlessness', and '3 ear-ossicles'. Why these characters, and why not others? Choice of characters in phylogenetic inference has traditionally varied according to focus. Vertebrate morphologists have, for instance, typically relied on muscles and skeletal structures, while invertebrate morphologists have focused on genitalia. More recent trends have tended toward characters based on neuroanatomical patterns and sperm morphologies (Wake 1994, p. 174). Since bones and muscles may have different patterns of similarity among taxa than do genitalia and neuroanatomical patterns, the most parsimonious hypothesis relative to some characters need not be the most parsimonious hypothesis relative to others.

But we might also include molecular characters in a data set. Should molecular data be considered in the same data set with morphological data? Michael J. Novacek explains the problem molecular data presents for parsimony considerations:

> . . . One of the most controversial issues in phylogenetics is whether or not data from diverse sources should be combined in a single data set. This approach is emphatically favored by Kluge . . . who advocates the incorporation of "total information" or "total evidence" as the valid source of phylogenies and classifications. Swofford . . . expressed concern that the independent contributions of different data sets will be obscured if they are combined . . . There are concerns that the huge numbers of characters resident in nucleotide sequences will simply swamp out the signal from a smaller set of albeit compelling morphological traits (Novacek 1994, p. 119).

What concerns Novacek and others, is that there are potentially many more characters at the molecular level. Each nucleotide in a DNA sequence could conceivably be regarded as a character, and a nucleotide substitution would then constitute an evolutionary change, just as the presence of a complex morphological structure—like ear-ossicles or chambered heart—would. But changes in the complex morphological characters typically used by morphological phylogeneticists hardly seem equivalent to a single nucleotide substitution. What is worrisome here, is that because the parsimony principle counts characters, the sheer quantity of the molecular data may render morphological data irrelevant. But as Novacek also suggests, some phylogeneticists believe that individual morphological traits can be better indicators of phylogeny. Furthermore, if morphological characters are the developmental consequences of the same

molecular characters, then in some sense the data set is redundant. Some characters seem to be counted more than once—as both a morphological and molecular character.

The use of behavioral characters likewise poses a challenge to the unequivocal application of cladistic parsimony. "Open mouth threat displays" in snakes (Greene 1994, p. 377), "orb-weaving" in spiders, and social behavior in wasps have all been employed in characters sets (Minelli 1993, p. 161). It is not at all obvious that a behavioral character is automatically comparable to either molecular or morphological characters. Schuh summarizes this dilemma, without proposing a solution.

> Traditionally, morphology at the macroscopic level has formed the basis for most recognized taxonomic characters. More recently, DNA and amino-acid sequences have become "standard" character sources for many groups, augmenting classical morphology. Behavior and products of behavior also enjoy a place as legitimate sources of character data. (Schuh 2000, p. 89).

It is possible, of course, to consider each type of character separately in independent data sets, but then there would be two or more parsimony determinations that may conflict—without a rule of resolution.

What is important here is that there is no algorithm for the formulation of the data set—no algorithm to determine which characters to include in parsimony considerations. Instead, background information about development, character change and evolutionary processes seems to influence the choice of characters. But also of particular interest here, tradition and training seem to play a role. This fact is of some importance, and I will be returning to it.

5. Character Individuation

Even if it were possible to formulate a rule prescribing the *types* of characters to include in a data set, cladistic parsimony would still be indeterminate because there is no single unequivocal way to identify and individuate characters. The character 'three ear-ossicles', for instance, can be regarded as one character, three characters, or even more. This has implications for the application of parsimony: one character would imply one change, three characters implies three changes. Other traits can be decomposed similarly, as some cladists recognize. Peter Ax, in his discussion of this problem, recognizes that the spiny coat of the Australian spiny anteater can be considered as either one character, or alternatively many characters—each spine being one character. If we regard the spiny coat as a single characteristic, then we might not place the spiny anteater and por-

cupine in a particular sister grouping. But if we regard each spine as a character, then given the number of spines possessed by each, we may be forced to infer that the anteater and porcupine are closely related. Ax rejects this possibility.

> . . . It is very evident that each single spine is a concrete structural part of the species which is very effective in defence. Nevertheless, a single spine cannot be recognized as a separable element in the pattern of features of the spiny anteater. That can only be done for the coat of spines in its totality (Ax 1987, p. 107).

Unfortunately, it is not clear what principle Ax is using to reject the possibility that each spine can be considered a character, and count as a similarity. Later, and in the passage quoted above, Ax suggests, without explanation, that characters or features must be *separable.* But it is not obvious what counts as separable. Perhaps he means only that anything that can be distinguished from other 'things' is separable. This criterion however, is far too weak. Individual spines can be distinguished, as can groups of spines ('tail spines' from 'back spines', for instance). Likewise, we can distinguish each ear ossicle, as well as the various structural features on each ear ossicle as characters (perhaps on the basis of shape, size, density, etc.). Separability, in this sense, shows little promise of providing an unambiguous character individuation criterion.[13]

Alternatively, character individuation could be based on function. A functional feature or complex would then be regarded as a character. Grande and Rieppel inquire after this possibility.

> . . . A functional morphological complex is composed of several structural components integrated into a common functional context. As the utility of such a structural complex for cladogram building is investigated, the question arises as to whether the whole functional complex should each be coded as a single character, or whether its component elements should be coded as separate characters (Grand and Rieppel 1994, p. 246).

Unfortunately Grand and Rieppel do not answer the question they raise, but it should be clear why a function-based individuation criterion cannot be unequivocal. An entire functional complex like three ear-ossicles can be individuated as a single character, functioning in hearing, while each

13. Nor is it obvious why our ability to distinguish features, or recognize them as "separable" should be relevant to whether a feature is a character or not. Character individuation would then seem to be an artifact of our constitution and not the constitution of the organism under consideration.

ossicle could also be individuated as a character, insofar as each ossicle has a function within that complex.

Grande and Rieppel are skeptical about the possibility of any principle of character individuation.

> What, after all, is a character, and how does it contribute to the search for patterns of relationship? Identification of a character starts with the perception of some similarity, but the phylogenetic information content of shared similarity is determined by congruence of characters . . . Since there is no theory-free observation, we can never know, in an objective way, what a "shared character" is (Rieppel and Grande 1994, p. 238).

This skepticism is echoed by Douglas Futuyma, relative to an independence criterion:

> Ideally one wants to decompose organisms into separate characters, each of which evolves independently of the others; then each character gives independent evidence of phylogenetic relations. Thus a superficially single character, such as number of teeth in a mammal, would more properly be refined into separate characters: number of incisors, canines, and so on. Conversely two seeming characters may be just two aspects of a single feature if they are consistently correlated; differences in shape are often simple consequences of differences in size, because of allometric growth and are not independently varying characteristics. But knowing what characters are independent is difficult in practice. Is each bristle on a fly a separate character, or all the bristles together a single character? And unit characters may be hard to define even conceptually. Developmental biology tells us that organisms consist not of independently formed unit characters, but of interacting developmental pathways, and the interactions among the pathways can themselves change in evolution (Futuyma 1979, p. 151).

So if separability, function, and independence fail to individuate characters unequivocally, is there no satisfactory concept of character to support the application of the parsimony principle? The failure to formulate a criterion of character individuation, raises concerns that character individuation, and therefore the application of parsimony, is either arbitrary or subjective.

There is, however, another sort of criterion that has been suggested—a criterion that focuses not on the intrinsic features of the individual organ-

isms themselves, but the phylogeneticists and the practices they engage in. E. O. Wiley argues for a communication criterion.

> In practical applications, a character is a part or attribute of an organism that may be described, figured, measured, weighed, counted, scored, or otherwise communicated by one biologist to other biologists (Wiley 1981, p. 8).

And,

> If one worker can communicate to another worker about an attribute or feature of an organism or a group of organisms, then the colleague is likely to be informed and consider the character as "real" (Wiley 1981, p. 116).

In this communication criterion, Wiley places the emphasis on social processes—communication and persuasion—rather than on the intrinsic traits of the organisms being compared. In a similar vein, Eldredge and Cracraft suggest a naming criterion. They first argue that the notion of a character is parasitic on the notion of similarity. Then they argue,

> . . . Similarities must be named, and it is these names that we call "attributes" or "characters" (Eldredge and Cracraft 1980, p. 43).

Since naming is a social process, like communicating, Eldredge and Cracraft have shifted the emphasis toward social process as well.

The first thing to notice about both the communication and naming criteria, is that they are also indeterminate. The character "three ear-ossicles" is comprised of three named characters—"malleus," "stapes," and "incus." There are therefore two inconsistent naming schemes, and two inconsistent character individuation schemes—without any apparent rule of resolution.[14] And surely if there are contradictory naming-based schemes, there can be contradictory communication-based schemes.

There is however, an intriguing suggestion in these last two criteria. Communication and naming are usually understood to be social processes accomplished by groups of individuals. On this suggestion, perhaps a feature of an organism is a character because phylogeneticists come to agree that it is a character. The application of cladistic parsimony, would

14. That there are three named characters composing "three-ear ossicles" might make us think it would be treated as three characters. Peter Ax, however, treats "three-ear ossicles" as one character with two character states—"three ossicles" is the derived state, and "one ossicle" is the ancestral state (Ax 1987, p. 145). Similarly, characters like "neural spines on cervical vertebrae 3–7 weak or absent" that can be decomposed similarly, have been treated as a single character (Novacek 1994, p. 105).

therefore be a consequence of what the group accepts as a character. This turn to social factors is reminiscent of Kuhn's claim that the best criterion of theory choice is the decision of a scientific group. It is also my next concern.

6. Character Exemplars, Pedagogy and Persuasion

In explaining his views on theory choice, Kuhn emphasized how his analysis could explain disagreement among scientists. The indeterminacy of values meant that two investigators could accept the same set of values, perhaps even agree about the priority of values, but still arrive at outcomes favoring different hypotheses. But Kuhn wanted to explain consensus as well. The notions of a 'paradigm' and 'normal science' presuppose that there is a community of scientists that can and do agree about a lot of things—including the application of values. And, it is true, that while there is disagreement about the application of cladistic parsimony, there is also some consensus.

This consensus is partly due to training: those phylogeneticists that come from the same background, tend to agree on the formulation of data sets, and to some degree the application of parsimony. Vertebrate morphologists typically turn to the same characters, as do invertebrate morphologists. Molecular phylogeneticists also tend to employ certain types of molecular traits in certain contexts, whether it be nucleotide, amino acid, or protein sequences. The consensus in all of these cases is due in part to pedagogical background. Those who study with vertebrate morphologists tend to recognize the same sorts of characters, at least partly because these are the characters they have learned to recognize.

Pedagogy plays an important role in Kuhn's analysis of science, in particular the practice of normal science.

> Close historical investigation of a given specialty at a given time discloses a set of recurrent and quasi-standard illustrations of various theories in their conceptual, observational and instrumental applications. These are the community's paradigms, revealed in its textbooks, lectures and laboratory exercises. By studying them and by practicing them, the members of the corresponding community learn their trade (Kuhn 1970, p. 43).

What the textbooks, lectures and laboratory exercise reveal, are standard examples—exemplars. A student-phylogeneticist learns to see characters when looking at standard examples of fish, birds, plants, etc. One way this is done, is through the use of *dichotomous keys* to teach the identification of taxa through morphological analysis.

A dichotomous key is a series of questions inquiring about the presence of various characters and character states. For instance, the key used to identify the genera within the Buttercup family first asks whether the flowers are radially or bilaterally symmetric—establishing flower symmetry as a character.[15] Then, depending on whether radial or bilateral symmetry is observed, other character states are used to distinguish the various genera. For instance, the key also asks if leaves are "opposite" or "alternate," petals are "fused" or "distinct," petals are "prominent" or "inconspicuous," sepals[16] are "spurred" or not, petals are "smaller than sepals" or not, and sepals are "showy" or not.

What is important here is that these keys present exemplars which establish a conceptual character scheme that guides observation. "Sepals spurred" and "petals fused" are standard examples of characters used to distinguish various Buttercup species. Kuhn has referred to similar taxonomic contexts to illustrate the role of exemplars in guiding observation and establishing similarity relations.

> . . . I ask that you imagine a small child on a walk with his father in a zoological garden. The child has previously learned to recognize birds and to discriminate robin redbreasts. During the afternoon now at hand, he will learn for the first time to identify swans, geese, and ducks. Anyone who has taught a child under such circumstances knows that the primary pedagogic tool is ostentasion . . . Father points to a bird, saying, "Look, Johnny, there's a swan." A short time later Johnny himself points to a bird, saying, "Daddy, another swan." He has not yet, however, learned what swans are and must be corrected: "No, Johnny, that's a goose." Johnny's next identification of a swan proves to be correct, but his next "goose" is, in fact, a duck, and he is again set straight. After a few more such encounters, however, each with its appropriate correction or reinforcement, Johnny's ability to identify these waterfowl is as great as his father's. Instruction has been quickly completed (Kuhn 1977, p. 309).

Kuhn then explains how this process works, by "highlighting" some features and "suppressing" others:

> By the end of the walk, features like the length and curvature of the swan's neck have been highlighted and others have been suppressed so that swan data match each other and differ from goose and duck

15. *Flora of North America* (1997).
16. Sepals are the leaf-like structures surrounding the petals.

> data as they had not before. Birds that had previously all looked alike (and also different) are now grouped in discrete clusters in perceptual space (Kuhn 1977, p. 310).

Kuhn concludes that

> Johnny, in short, has learned to apply symbolic labels to nature without anything like definitions or correspondence rules. In their absence he employs a learned but nonetheless primitive perception of similarity and difference. While acquiring the perception, he has learned something about nature. This knowledge can thereafter be embedded, not in generalization or rules, but in the similarity relationship itself (Kuhn 1977, p. 312).

This process is grounded in the functioning of exemplars.

> Need I now say that the swans, geese, and ducks which Johnny encountered during his walk with father were what I have been calling exemplars? Presented to Johnny with their labels attached, they were solutions to a problem that the members of his prospective community had already resolved. Assimilating them is part of the socialization procedure by which Johnny is made part of that community and, in the process, learns about the world which the community inhabits. Johnny is, of course, no scientist, nor is what he has learned yet science. But he may well become a scientist, and the technique employed on his walk will still be viable. That he does, in fact, use it will be most obvious if he becomes a taxonomist. The herbaria, without which no botanist can function, are storehouses for professional exemplars, and their history is coextensive with that of the discipline they support (Kuhn 1977, p. 313).

In these passages, Kuhn identifies individual organisms as exemplars, but characters can also function as exemplars. The particular spurred sepals found in an individual plant, can function as an exemplar of 'sepals spurred' just as the individual plant itself can serve as an exemplar of *Ranunculacae* (Crowfoot family), and just as the curve of a neck can function as an exemplar of the characters that distinguish swans and ducks.

There are several facts worth emphasizing. First, the exemplary characters used in the dichotomous keys to identify taxa, may also function in phylogenetic analysis. The presence of spurs in sepals might constitute a hypothetical evolutionary change that counts in parsimony considerations. Second, these characters could be individuated in different ways. "Sepals showy," for instance refers to the size and coloration of the sepals, and

could be individuated as multiple characters—in terms of the intensity of color, hue, pattern of coloration, and size. Finally, the character scheme presented in the key represents a *tradition* of character individuation—standard examples accepted by the community as paradigmatic. There could conceivably be a different tradition of character individuation, with different parsimony implications.

But it should also be recognized that the tradition of character individuation is not static and unchanging. Most obviously, new molecular characters are becoming part of the tradition, as are new morphological characters, characters perhaps based on newly discovered genetic linkages or developmental fields. Wiley, in explaining his communication criterion, does not explicitly address the introduction of new characters. But when he claims that "if one worker can communicate to another worker about an attribute or feature of an organism," surely he is not just referring to an attempt at communication, but a process of persuasion. Following Kuhn here, we might suspect that this communication is a matter of convincing others to accept new exemplars, perhaps even molecular exemplars.[17]

Wiley's communication criterion now makes more sense. For Wiley, what counts as a character is that which you can persuade others within your community to accept as a character. Techniques of persuasion therefore become important. But it is here that the charge of 'mob psychology' has some bite. How do you convince colleagues to accept a particular character individuation scheme—as illustrated in a particular exemplar? Kuhn's critics seem to assume, perhaps uncharitably, that "persuasion" means coercion—the use of political power to force others to see things your way. Persuasion might then involve the rejection of dissident papers for publication in professional journals, or the denial of tenure to those who don't *see* things your way. Kuhn describes this "might makes right" interpretation.

> Members of a scientific community can, I am held to have claimed, believe anything they please if only they will first decide what they agree about and then enforce it both on their colleagues and on nature. The factors which determine what they do choose to believe are fundamentally irrational, matters of accident and personal taste. Neither logic nor observation nor good reason is implicated in theory-choice (Kuhn 1970, p. 260).

17. Perhaps persuasion might involve convincing others to see an analogy between a character and a character exemplar.

But for Kuhn, persuasion does not *simply* mean the application of political force. There may still be good reasons—based on logic and observation—for the particular application of a value.

> What I am denying then is neither the existence of good reasons nor that these reasons are of the sort usually described. I am, however, insisting that such reasons constituted values to be used in making choices rather than rules of choice (Kuhn 1970, p. 262).

The possibility that good reasons might function in theory choice seems to be the basis for Kuhn's denial that it is mere mob psychology that is at work here.

In order to evaluate Kuhn's defense relative to cladistic parsimony, we would need to take a much closer look at the processes that govern the acceptance of character exemplars in phylogenetic inference. This is beyond the scope of this paper so I will not be able to comment on the mob psychology charge, except to say that if characters represent evolutionary events, then what should be significant in exemplar choice are precisely those factors that can be used to correlate characters with events—evolutionary changes. A character individuation scheme is, in some sense, an event hypothesis. For instance, if three ear-ossicles is taken to indicate a particular phylogenetic hypothesis of sister grouping, then it is because that feature we identify by the name three ear-ossicles is taken to have originated in the immediate common ancestor of some sister taxa. However that event hypothesis is to be determined, because of the complexity of evolutionary processes, it is surely not by the application of an algorithm or rule.

7. Conclusion

The indeterminacy Kuhn describes in the application of scientific values is apparent in the application of cladistic parsimony, because of indeterminacy in both the formulation of data sets and the individuation of characters. Kuhn was aware, as are we, however, that one example of value indeterminacy cannot establish a general claim about theory choice, any more than the observation of a single black raven can establish a general claim about the color of ravens. And we should also be wary of describing the practice of science just so that we can emphasize those characteristics that would seem to confirm a particular historical theory such as Kuhn's. But surely the fact that Kuhn's account of theory choice accurately predicts the indeterminacy in cladistic parsimony is a virtue of that account.

The fruitfulness of Kuhn's account of theory choice is also apparent. As long as we regarded cladistic parsimony as an unequivocal rule of theory

evaluation, the disagreement among phylogeneticists was not easily explicable. There is no disagreement about simple addition, why should there be disagreement about the application of parsimony—if it were merely the counting of assumed evolutionary changes? The recognition of indeterminacy in cladistic parsimony is presupposed by any investigation into the causes of that indeterminacy. If we believe cladistic parsimony is unequivocal, we shall never fully understand the role of character individuation in its application.

Kuhn's account has been fruitful in yet another way. By understanding character individuation as based on standard examples—exemplars—we can understand why taxonomists and phylogeneticists can recognize characters without being able to formulate a criterion of character individuation. This paradox is recognized by Wiley.

> The term "character" is used by every taxonomist. . . . I have talked to no taxonomist who did not have an intuitive idea about what characters are and there has been little or no confusion in taxonomists communicating their ideas about characters. Yet the term is usually defined in an inadequate manner (Wiley 1981, p. 115).

If Kuhn is right, 'character' cannot be defined because individual characters are identified and individuated by reference to exemplars—which are examples, not definitions.[18]

The fact that I cannot here give a satisfactory account of why organisms get schematized into the character schemes they do, means that I cannot assess the charge of mob psychology as it might apply to cladistic parsimony. That characters may be accepted as discrete characters merely on the basis of tradition and persuasion is of some concern. And some acts of persuasion, which lead to group decisions, may even be described as "might makes right." Surely there is at least some arbitrariness in character individuation. But reasons can be given, and often are, for the acceptance or rejection of each character individuation scheme. What these reasons are, and how they function in exemplar choice and character individuation, is surely worthy of further investigation.

18. Kuhn claims that even if we could formulate a definition, we would be embarked on a different project: "The philosopher is at liberty to substitute rules for examples and, at least in principle, he can expect to succeed in doing so. In the process, however, he will alter the nature of the knowledge possessed by the community from which his examples were drawn. What he will be doing, in effect, is to substitute one means of data processing for another. Unless he is extraordinarily careful he will weaken the community's cognition by doing so. Even with care, he will change the nature of the community's future responses to some experimental stimuli" (Kuhn 1977, p. 314).

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