PARSIMONY PRINCIPLES IN PHYLOGENETIC SYSTEMATICS: A CRITICAL RE-APPRAISAL.

by: ROSEMARY JOHNSON, Division of Life Sciences, Scarborough College, University of Toronto, 1265 Military Trail, West Hill, Ontario, Canada, M1C 1A4.

Received June 19, 1981; August 12, 1982

ABSTRACT: Principles of parsimony have traditionally been the subject of intense study by logicians and philosophers of science. As a result, the concept of parsimony currently acceptable in the formal sciences is a highly refined, non-axiomatic principle whose application is rigorously restricted. Although such a foundation is often implied, this coherent and analytical view of parsimony has no counterpart in evolutionary biology, where the principle has been used in the reconstruction of phylogenies. Parsimony in phylogenetic systematics is instead a chameleon concept, used indiscriminately to identify any one of a series of ill-defined and seemingly contradictory notions. In this paper a review of the formal precepts of parsimony is presented as a background for evaluating the use and justification of the principle in phylogenetic systematics. It is suggested that a thorough re-appraisal of the value of parsimony in the reconstruction of phylogenies should preface its continued use.

* * *

INTRODUCTION

As in all science, the importance of standardization to the methods of evolutionary biology is beyond question. A clear statement of the rationale for, and implications of, a particular procedure is crucial however, not only in the introduction of new methods, but also in the periodic re-examinations to which popular or established methods should be subject. For the last decade, the relevance of philosophical and logical tenets in re-appraising ill-founded, outmoded or altered evolutionary concepts has been repeatedly stressed by phylogeneticists (ex., Bock, 1973; Eldredge and Cracraft 1980; Kitts 1977; Wiley 1975), a prescription that has been used to good effect in attempts to standardize procedures in other aspects of science. For example, the metamorphosis of the deductive argument of logic into the hypothetico-deductive method of empirical science (Popper 1968a, 1968b), provided an unambiguous general criterion for evaluating the scientific nature of hypotheses.

Parsimony is a concept to which the preceding remarks are relevant. Principles of parsimony in systematics have been employed both to produce and to evaluate reconstructions of phylogeny (Camin and Sokal 1965; Eldredge and Cracraft 1980; Engelmann and Wiley 1977; Farris 1978; Lundberg 1973; Platnick and Nelson 1978), procedures that have been criticized (Bonde 1975, 1976; Inger 1967; Jardine 1972; Kitts 1981; Kohlberger 1978; Patterson 1978) to some extent. Recently Dunbar (1980) and Holsinger (1981) have discussed in more general terms the use of the principle in the natural sciences. The fundamental properties of parsimony have also been investigated extensively by philosophers of science and logicians (Bunge 1961; Goodman 1959, Kemeny 1955; Popper 1968a, 1968b; Quine 1963), with the intention of reducing inappropriate multiple usage by producing a set of formally valid methodological rules. The relevance of similar successful standardization in the use and justification of parsimony in phylogenetic systematics is obvious. It is the purpose of this communication to attempt to identify current untenable pluralism in the use and justification of parsimony in phylogenetic reconstruction.

Parsimony

Frequently invoked but seldom defined, parsimony is a concept which embodies the notion of frugality or absence of superfluity. Parsimony has been defined as "the avoidance of waste" (fifth edition, Pocket Oxford Dictionary 1969), and "economy in the use of a specific means to an end" (third edition, Webster's New International

* * * * * * *

Evolutionary Theory 6: 79-90 (September, 1982)
The editors thank E. Sober and two other referees for help in evaluating this paper.

Dictionary 1963). Kohlberger (1978) advocated general substitution of the term "economy" for parsimony, to distinguish between the formulations of the fourteenth century Franciscan monk William of Ockham ("Ockham's razor") and those of modern systematists. However, in the present work the historical distinctions between concepts of parsimony are not considered relevant, and economy, parsimony and simplicity are used as synonyms.

FORMAL ASPECTS OF PARSIMONY

The wariness with which philosophers of science have approached the study of parsimony appears to be due to recognition that traditionally, parsimony has had more than one accepted meaning. Bunge (1961) for example, described four kinds of theoretical simplicity. Repeated attempts to generate an inclusive definition of parsimony have thus generally not been successful, although this has not been considered an insurmountable obstacle to the study of the concept. As Hempel (1966, p. 42) noted, "The question of criteria of simplicity has in recent years received a good deal of attention from logicians and philosophers, and some interesting results have been obtained, but no satisfactory general characterization of simplicity is available .... However, there certainly are cases in which, even in the absence of explicit criteria, investigators would be in substantial agreement about which of two competing hypotheses or theories is the simpler."

The more productive alternative has been the acceptance of parsimony as a noun which must be qualified. Most of the philosophical literature deals therefore with the categorization of parsimony - i.e., the definition of various types of parsimony and the analysis of the spheres of influence of each type (see for example, Friedman 1972; Good 1968, 1974; Manders 1976; Priest 1976; Rolston 1976).

For the purposes of the present work, Rudner's (1961) categorization according to the manner in which concepts of economy are utilized is relevant. Rudner distinguished two basic usages of parsimony - ontological (extra-linguistic) and descriptional (linguistic). The difference between ontological and descriptive parsimony is analogous to that between the empirical (e.g. physics, biology, geology, etc.) and formal (mathematics, logic) sciences respectively. The procedures of the former deal with physical processes and properties, while those of the latter are determined by convention and consensus.

Similarly, ontological parsimony is simplicity of phenomenon - in an ontological sense, a simpler hypothesis invokes the action of fewer physical entities. Ontological use of parsimony involves the attribution of economical properties to features or processes of the universe, either independently (objective-ontological) or as a function (subjective-ontological) of the perception of the observer. Identification of ontological parsimony derives from demonstrative or empirical concerns, i.e., from documentation of the extent to which a process or feature can be shown to conform to some agreed standard of economy. For example, salt may be produced either by bonding sodium directly with chloride or by mixing compounds containing these elements. The process may be said in the former case to be ontologically more parsimonious - if economy is measured in terms of minimizing waste products. In a phylogenetic context alternate views of the geneological relationships among specific groups can also be compared with respect to degree of ontolologic parsimony if, say, parsimony is measured in terms of numbers of separate genetic events required to produce a particular phylogenetic pattern. For example, if the amniotic egg arose only once, so that all amniotes are descendents of the same ancestral group, then this phylogeny is ontologically more parsimonious than one (in an alternate universe) in which amniotes are polyphyletic through the multiple development of such eggs. Provided that a suitable definition of economy can be agreed upon, this specific and restricted usage of parsimony is relatively unproblematic. Generalization of ontological parsimony has, by contrast, been the subject of such stringent criticism that condemnation of the procedure by philosophers of science has been virtually unanimous. Kapp (1958) appears to be an exception. As with any other hypothesis of empirical science, ad hoc elevation of ontological parsimony to the status of an axiom has especially been attacked. Harré (1972, p. 45) summarized these views by commenting, "There can be no doubt that the history of science shows that the laws of nature are always more complex than we originally thought. The Principle of Simplicity as a blanket principle can hardly be accepted. Of course at each stage of knowledge it would be mad to choose any more complex hypothesis than one has to, but that is hardly a methodological principle of the portentious epistemological status assigned to the principle of simplicity." Salmon (1961, p. 275) was equally succinct in asking, "Why should we believe that a simpler hypothesis is more likely to be true than a complex one, given that each has sufficient explanatory power with respect to the facts in question? ... Is there, as some scientists seem to have believed, a metaphysical assumption or principle, presupposed by science, to the effect that the universe is fundamentally simple? If so, what reason could we have for accepting such a presupposition? To say that science has tended to confirm this assumption is to make the assumption a sort of super-hypothesis which is, itself, subject to the same kinds of problems as any other hypothesis. To deny that this assumption is a hypothesis like any other scientific hypothesis is to make it either empty or a synthetic a priori truth."

The crux of the problem identified by both Harré and Salmon is an unremmiting thorn in the side of empirical science - the reconstruction of unobserved or unobservable events - and the phylogenetic example previously given illustrates the two major difficulties with using ontological parsimony in an attempt to resolve it. In phylogenetic reconstruction, processes (such as parallelism, direct descent and convergence) which differ in their degree of ontologic parsimony are known to produce similar results. If degree of parsimony is used as a basis for choosing one pathway as closer to the course of events, then the degree of parsimony must first be allied with the frequency with which it has been documented to occur. Failure to provide this crucial justification renders the argument immediately susceptable to the criticisms of Harré and Salmon. However, neither provision nor acceptance of this documentation entirely resolves the problem. Empirical axiomatization of parsimony (e.g., confirmation of Salmon's "super-hypothesis" through accumulation of accredited specific instances) introduces the second difficulty, generally (though not indisputably - Ackermann, 1961) discussed under the rubric of 'inductive simplicity'. The rationale for uniting parsimony with induction was outlined by Foster and Martin (1966, p. 238) who suggested, "It is argued that we use simple theories because these theories in the past have usually turned out to be correct and we can infer by an inductive generalization that they are likely to continue to be usually correct." However, as these authors, Popper (1968a, 1968b) and Quine (1963) noted, justification of an inductive inference necessitates the untestable assumption of future or past uniformity. The preceding criticism (christened 'Hume's Problem' in honour of the philosopher who first attempted a detailed analysis of the problem) has been the center of an unabating storm in philosophy for the past two centuries. The opposing factions, aligned into inductivist and deductivist camps, continue to exist in a state of intermittent combat, despite repeated claims of ultimate victory by champions of either side. Inductive simplicity is thus considered justifiable by Carnap (1952), Priest (1976) and Reichenbach (1938), unjustifiable by Ackermann (1961) Barker (1961b) and Hempel (1966) and irresolvable by Rudner (1961).

Although this conflict is independent of the association between degree of parsimony and the frequency with which it occurs (i.e., the criticism stands whether the greatest or least degree of parsimony is chosen as most likely), the most frequently encountered form of the "super-hypothesis" accords the greatest liklihood to the most parsimonious pathway. In discussing this phenomenon, Hesse (1974, p. 257) provided grounds for rejecting the notion by noting that, "... in the case of simplicity there are clear counter-examples where the simplest theory has not proved successful: the planets do not move in circles; Newton's law of composition of velocities is false; protons and electrons are not the two irreducible elements which constitute all matter ..."

Hesse also recognized the potential overlap in objective- and subjective-ontological parsimony in continuing, "... it may be that the sample of simple laws we do believe to be successful is not unbiased, for it may represent just that aspect of nature which has been found sufficiently simple to be manageable to the human mind, and no conclusion can be drawn from it to the rest of nature."

A very different situation prevails with respect to the descriptive use of parsimony. Descriptive parsimony is linguistic simplicity - in a descriptive sense a simpler hypothesis is one which is expressed more economically. Linguistic parsimony deals with some aspect of the form of a correct argument, while ontologic parsimony deals with some aspect of the content of the argument. Like ontologic parsimony however, descriptive simplicity is subdivided into a number of categories (Rudner, 1961).

Simplicity is used in a descriptive-notational sense to represent some feature relevant to the manipulation of a description, such as its length (objective-notational) or ease of handling (subjective-notational). Descriptive-logical use of parsimony relates to the role of simplicity in the procedures of argument or reasoning and is in turn subdivided into objective-logical and subjective-logical simplicity. Of the four types of descriptive simplicity, only one has received any great attention from logicians and philosophers of science. Both subjective-notational and subjective-logical simplicity (i.e. psychological response to formal simplicity) appear generally to be considered outside the philosophy of science, while objective-notational usage is regarded as trivial (Rudner 1961). In contrast, objective-logical parsimony is an area of intense activity, and many interesting and productive advances have been made in the past few decades. There are several foci in the study of objective-logical simplicity. Goodman (1943, 1949, 1950, 1951, 1952, 1955a, 1955b, 1959, 1961) is the protagonist of the most widely accepted school, which is concerned with the simplicity with which information is presented in the predicate bases of hypotheses. In general terms, Goodman presented arguments that the simplest sets of predicate bases are those which cannot be replaced by any other set. The degree to which predicate bases can be reciprocally substituted is therefore a measure of their degree of simplicity. The Goodman calculus of simplicity is a means of investigating the organization or structure of competing theories (Hillman 1962). Simplicity is systematization (Goodman 1959) - it is a means of evaluating redundancy and irrelevancy in different hypotheses, and thus it constitutes an advance in the standardization of scientific method.

In a different vein, Popper (1968a, 1968b), who is noted for the promotion of the hypothetico-deductive method of empirical science (whereby hypotheses are evaluated by testing, or attempting to disprove or falsify the predictions deduced from them) created a relationship between this method and parsimony by equating simplicity with the degree of falsifiability of an hypothesis. By this definition the simplest theories are the most falsifiable because "they tell us more; because their empirical content is greater and because they are better testable" (Popper 1968b, p. 142). It should be noted that this ad hoc synonymy of parsimony and falsifiability is contrary to the current consensus on the meaning of descriptive parsimony and is worth mentioning only because of the regard in which Popper appears to be held by many phylogenetic systematists. This unorthodox usage may in fact be responsible for much of the confusion surrounding the application of parsimony in evolutionary biology (see below).

The properties of descriptive parsimony have similarly, though to varying degrees, concerned Barker (1961a, 1961b), Carnap (1952), Hempel (1966), Jeffreys and Wrinch (1921), Kemeny (1953), Priest (1976), Quine (1963, 1966), Reichenbach (1938) and Schlesinger (1960a, 1960b), among others. Recently Sober (1975) attempted to relate the descriptive simplicity of hypotheses to their degree of 'informativeness' (i.e., the simplest hypothesis represents the most inclusive summary of the properties of specific entities covered by the hypothesis), a prescription that appears to contain elements of both Goodman's and Popper's analyses of parsimony.

It should be emphasized that justification of descriptively simpler hypotheses on the grounds of increased informativeness, falsifiability or the degree to which they systematize a body of data is quite independent of the truth of the hypothesis. Unlike ontological parsimony, descriptive parsimony has no epistemological or empirical component - it cannot be used to 'test' the veracity of an hypothesis. As Salmon (1973) commented, "logic deals with the relation between premises and conclusion, not with the truth of the premises" (author's italics). The difficulty engendered by confusing these aspects of parsimony can be illustrated by reference to 'curve-fitting' problems. Ackermann (1961, p. 152) described curve-fitting as, "allowing experimental observations to be represented by points on a real plane, but the alternative hypotheses invoked to explain these observations to be represented by curves drawn through the plane. In this simple model a satisfactory hypothesis is represented by a curve passing through or very near to, each designated point in the plane. It is at once obvious that many curves can be drawn so as to satisfy this intuitive criterion. But science, so it is said, can only accept one. We may solve that problem ... by drawing the simplest curve through the points and accepting that as representing the hypothesis that science accepts." In this instance empirical testing has left several satisfactory hypotheses which vary in their degree of descriptive simplicity. Rejection of alternate hypotheses on the basis of descriptive parsimony does indeed permit a choice to be made, but one which lacks empirical or predictive credibility. The sterility of such an approach was noted by Ackermann, who continued, "This is, however, but the description of a solution that can be no better than the notion of simplicity involved." A phylogenetic analog to the curve-fitting problem would be, for example, the situation in which observations considered indicative of relationships among taxa are represented as points on a plane. As in Ackermann's example many curves (representing hypotheses of relationship) may be drawn through these points: the uncertainty traditionally associated with the interpretation of historical events rarely permits any greater empirical refinement. The curves do vary in their degree of descriptive simplicity - with the simplest curve described, say, by equations in which variables appear only once (no convergence or parallelism) and the number of hypothetical intermediates is restricted. Descriptive parsimony may be used here, as in the previous example, as a kind of deus ex machina preventing the embarassment of multiple acceptable explanations, but the price, as Ackermann has noted, is abrogation of empirical significance.

Two issues appear to be fundamental to the curve-fitting problem described by Ackermann. The first concerns the methodological axiom that but one solution is acceptable to 'science '. This idea is so pervasive among scientists that, as in Ackermann's statement, it appears to require no explanation. In view of the frequency with which a number of hypotheses remain viable after a period of empirical testing, critical re-evaluation of this concept appears to be warranted. Although a single surviving hypothesis is traditionally the preferred result of scientific endeavour, it would perhaps be more appropriate to view this as an ideal to be pursued rather than as an unalterable dictum. Commitment to the provision of a single solution in instances where no empirical tests are conclusive leads to the second issue relevant to curve-fitting - the provision of a criterion by which a choice may be made. The choice, as described above, is usually based on some non-evidential criterion (such as descriptive parsimony) but the use of such a criterion to decide which hypothesis should be accepted (however provisionally) as the most accurate representation of the experienced world sets a dangerous precedent in the evaluation of scientific evidence.

PARSIMONY IN PHYLOGENETIC SYSTEMATICS

Evaluation of the use of parsimony principles in phylogenetic systematics is complicated for a number of reasons. First, the sense (i.e., ontological or descriptive) in which parsimony is applied is not always clear - in fact the term is invariably used without any qualification whatsoever. Marshall (1977), Rosen (1974) and Simon (1979), for example, avoided both identifying and justifying the term by using parsimony without any explicit reference to a relationship between economy and genealogy. Estabrook (1972, p. 451), in reviewing the relationship between simplicity and the computational techniques advocated earlier by proponents of numerical parsimony implied that parsimony was widely used in an ontologic sense by commenting "The basic idea of parsimony common to the methods just discussed suggests that estimates of evolutionary history which imply a minimum of 'evolution', appropriately quantified, can be expected to be good. The origin of the idea of minimum evolution is difficult to establish ... I suspect that it has served for years as a tacit assumption in the practice of estimating the evolutionary history for particular groups."

It could be argued from this that the majority of phylogeneticists are unaware that there is a critical distinction between ontological and descriptive parsimony. However, some phylogeneticists (Bonde 1976; Jardine 1972; Patterson 1978) have themselves identified some of the difficulties associated with generalized ontological use of parsimony, which perhaps explains the almost routine inclusion now of a disclaimer of ontological significance. Wiley (1975, p. 236), for example, suggested that the process of evaluating an hypothesis, "be done under the rules of parsimony, not because nature is parsimonious, but because only parsimonious hypotheses can be defended by the investigator without resorting to authoritarianism or apriorism," a view which was endorsed by Cracraft and Eldredge (1979). Earlier, Cavalli-Sforza and Edwards (1967, p. 555) in criticising (as a teleology) the Camin and Sokal (1965) assumption that nature is parsimonious, defended their own method as "... the intuitive idea that a plausible estimate of the projection of the evolutionary tree onto the 'now' plane is given by that tree which invokes the minimum total amount of evolution." However, a total absence of further explanation conspires to frustrate attempts to dissect the sense in which parsimony is used here. Wiley's claim is difficult to analyse as no information was given by which the rules (criteria?) of parsimony were to be identified, nor were the logical relationships between the hypothesis, the means of evaluation and the rules of parsimony explained. In addition, the justification of (?descriptive) parsimony as a concept devoid of "authoritarianism" and "apriorism" cannot, in the absence of further explanation, be accepted as valid in view of the criticisms of Ackermann (1961), Foster and Martin (1966) and Quine (1963), summarized above. The situation is still less satisfactory in the Cavalli-Sforza and Edwards account of phylogenetic parsimony. Even if Kaplan's (1964) characterization of intuition as "unreconstructed logic in use" were admitted as valid, the Cavalli-Sforza and Edwards defense is so vague that it virtually defies analysis. Without further comment by the authors, the meaning of "minimum total amount of evolution" is difficult to perceive if ontological parsimony has already been rejected. The confusion is increased by the fact that the properties of the method clearly puzzled its progenitors, who admitted (1967, p. 555) that "the assumptions underlying this method are not too clear .... its success is probably due to the closeness of the solution it gives to the projection of the 'maximum-likelihood' tree. The extent of the similarity merits further investigation and experience with simulated trees should clarify its logical status."

Despite this irritating semantic confusion, there does appear to be a general sensitivity among phylogeneticists to the problems associated with ontologic parsimony. Mitter (1981, p. 373) recently summarized this view in commenting, "Recent discussions of cladistic method by zoologists have been marked by a strong philosophical flavour, with workers attempting to defend particular methods as optimal on the grounds that they correspond to some general philosophical criterion for choosing among scientific theories. There is widespread (but not universal) agreement that (a) systematic methods should be as free as possible from assumptions about how evolution works, since these assumptions are in general not testable without reference to systematic results, and (b) that the appropriate philosophical criterion is parsimony of explanation, from which many workers have deduced grouping by synapomorphy [shared derived characters] as the most desirable method." It would seem then that there is no problem with phylogenetic use of parsimony, as the concept described by Mitter as acceptable to phylogeneticists appears to be the relatively unproblematic descriptive parsimony favored by philosophers of science. However this harmony in meaning is misleading - there is instead widespread confusion in evolutionary biology over the identification of descriptive parsimony and, more seriously, its domain. Although many phylogeneticists (e.g., Engelmann and Wiley 1977; Harper and Platnick 1978; Platnick 1977a; Platnick and Nelson 1978) have purported to employ Popper's criterion of parsimony, closer inspection reveals serious discrepancies. Acceptance of

Popper's formulation of parsimony (see above) categorically denies simplicity any role in evaluating the relative merits of competing hypotheses as conjectures about the world of experience. Popperian parsimony is an objective-logical device. It is a criterion for distinguishing between hypotheses on the basis of their formal structure; it is a description, not a test, of the content of an hypothesis. The level at which Popperian parsimony adjudicates between competing hypotheses is that of hypothesis formation, a point previously noted by Bonde (1975, 1976) and Patterson (1978). Popperian parsimony simply gives a sequence for the testing of hypotheses - simplest first. As the accuracy of an hypothesis is tested using empirical criteria, the result of the test (the "explanation") is independent of the parsimony of the hypothesis. There are thus two phases of choice in Popper's method: the first is an objective-logical procedure in which parsimony plays a critical role, while the second is an empirical procedure to which parsimony is irrelevant. Utilization of Popper's criterion of parsimony produces hypotheses that are better corroborable, not corroborated, as suggested by Engelmann and Wiley (1977). The distinction cannot be overemphasized. Wiley is particularly inconsistent in his use of parsimony: the manner in which parsimony is described and applied in his contributions of 1975 and 1977 (with Engelmann) is in sharp contrast to an admonition in 1976 (p. 10) that "parsimony does not constitute a test of a scientific hypothesis." If these authors were using Parsimony in an objective-logical sense the initial (parsimonious) ordering of hypotheses would be followed by an account of the empirical tests applied and a discussion of the results. However, perusal of these papers shows that the analysis stops when the hypotheses of relationship have been ranked by relative parsimony, so the "requirement" has here usurped the function of a test and become the ultimate arbiter. This point was made unequivocally evident when Engelmann and Wiley (1977, p. 6) stated, "When various tests conflict and there is no hypothesis available that is not refuted, we must assume that some of our characters are mistakenly identified or do not provide valid tests at the level of the problem at hand. By applying the criterion of parsimony we may select the hypothesis which includes the fewest internal inconsistencies (errors) and therefore requires the fewest *ad hoc* statements (Popper, 1968a: 145). Since such statements of error, unlike statements of identity, are untestable, we are minimizing the number of untestable assumptions in our hypothesis of relationships. Thus, the most parsimonious of two or more hypotheses is the more highly corroborated one." The clearly *a posteriori* nature of this procedure emphasizes the fundamental misunderstanding these authors have of Popper's *a priori* criterion. Platnick and Nelson, in a similar vein (1978, p. 5), suggested that an untestable hypothesis might be made "scientific" (*sensu* Popper) utilizing "a methodological rule that requires us to choose the most parsimonious hypothesis of relationship that will account for any given set of character distributions ", while Platnick (1977a, 1977b) advocated the use of parsimony principles to 'test' reconstructions of phylogeny under the aegis of the hypothetico-deductive method. The most cogent criticism of this attitude came not from Popper but from Bunge (1961, p. 127) who stated, "The simpler theories are easier tested both by experience and by further theories i.e. by inclusion in or fitting with contiguous systems. Syntactical and semantical simplification are, then, sufficient to improve testability even though they are not strictly necessary to secure it. Yet, there is as great a distance between testable and tested, as there is between a promise and its fulfilment. Syntactical and semantical simplicity are relevant to the likelihood of scientific theories in so far as they are factors of both systematicity and testability. But the assessment of the degree of likelihood of a theory is one thing, and the estimate of its degree of corroboration is another: the latter is done *a posteriori*, after certain tests have been given ... It is only in the prior estimate of the likelihood of a theory that considerations of simplicity can legitimately arise, and this in an indirect way, namely, through the contribution of simplicity to systematicity and testability."

In any event, Popper's view of parsimony is only one among many in the philosophy of science so even correct application of his concept is not representative of the philosophical consensus (see above).

Even more serious discrepancies in the identification of descriptive simplicity are apparent when parsimony is used in a manner superficially related to Rudner's objective-notational utilization i.e., when features such as the number of branching points are applied to a comparison of reconstructed phylogenies. The length of a reconstructed phylogeny has been considered a function of both qualitative and quantitative assessment of, for example, morphological or molecular similarity (Mikevich and Johnson 1976), geographical range (Platnick and Nelson 1978) and recency of ancestry (Engelmann and Wiley 1977). The length of an hypothesis is generally regarded as a subject of trivial interest by philosophers of science. Rudner (1961, p. 177) suggested that "such an obvious objective characteristic of a formulation as its length, seems wholely uninteresting .... Patently, with the relevant qualifications, a hypothesis with _n_ parametric expressions is _shorter_ than n + 1. Again, patently, it seems sensible to speak of such shorter hypotheses as being objectively notationally more simple than the longer ones. But (as Goodman points out) any hypothesis is trivially reducible to one of minimum length, i.e. may be formulated in as brief notational compass as any other." The reducibility that Rudner discussed is a function of logical conjunction whereby a series of statements may be reduced to one (albeit lengthy) statement by the application of suitable connectives. The phylogenetic analogue could be said to be the postulation of a single macroevolutionary event to provide the most parsimonious account of all observable taxonomic or character variation, but the resemblance here to notational simplicity is misleading, as the length of a particular phylogeny is not a linguistic function. Although it would seem to be somewhat unnecessary to note that the sequence and results of genealogical events are influenced neither by convention nor consensus (so that phylogeny is no less a physical phenomenon than orogeny), improper identification of the _ontological nature of phylogeny_ appears to be the greatest single source of confusion in both the application and justification of parsimony in systematics, a point also noted by Kitts (1981). For example, in a review of Sobers' (1975) perception of simplicity, the role of parsimony in phylogenetic systematics was defined as follows by Beatty and Fink (1979, p. 647): "In systematics, questions of parsimony most commonly arise with regard to alternative cladistic (genealogical) accounts of the similarities and differences of several taxa. That is, data describing the similarities and differences of several taxa equally support a number of different hypotheses as to the genealogical relationships of the taxa. Therefore, some criterion other than evidential support is needed to decide among the competing hypotheses. And, the criterion frequently chosen is parsimony - i.e., the most parsimonious hypothesis is provisionally accepted. Generally, the hypothesis considered most parsimonious is the one which, in conjunction with the fewest phenotypic evolutionary steps, accounts for the similarities and differences of the taxa in question." Hecht (1976, p. 348) in an earlier version of the same theme, apparently regarded this prescription as axiomatic when, without further explanation or justification, he asserted "In arranging a set of taxa that have been compared across morphoclines, it should be possible to reconstruct the phylogenetic pathway by looking for the most reasonable set of relationships utilizing the simplest or most parsimonious explanation" and added that the most parsimonious argument, in conjunction with some criterion of weighting was capable of determining "the most probable phylogenetic scheme." In other incarnations (with and without weighting criteria) similar sentiments can be attributed to Ashlock (1974), Camin and Sokal (1965) and Nelson (1973). The core of the problem here, as in the "curve-fitting" example described previously, is that the empirical evidence is equivocal, producing multiple acceptable solutions, so an ad hoc non-empirical criterion must be introduced - simply to permit a choice to be made. For example, Szalay (1977, p. 17) accepted Hecht's (1976) view of parsimony and added, "should this call for parsimony not be heeded then nothing prevents one from postulating _any_ phylogenetic hypothesis." It is evident from the subsequent discussion that "postulating" comprises aspects of hypothesis evaluation in addition to hypothesis formation, yet this essentially empirical procedure relies on a principle of parsimony whose sole justification is the prevention of an impasse. The situation was doubly confounded by Beatty and Fink, for although it is evident elsewhere ("The reasons for calling a linguistic description simple are different from the reasons for calling the phenomenon it describes simple." p. 643) that these authors are aware of the dichotomous nature of ontological and descriptive parsimony, the proviso of "fewest phenotypic evolutionary steps" attached to the suggested non-evidential criterion creates a hybrid concept with none of the strengths of the original ideas. In each case the result of this procedure is the same - a choice has been made, but it is totally lacking in empirical credibility.

The confusion in justificatory modes engendered by overlapping the domains of different types of parsimony is particularly evident in the work of some proponents of numerical parsimony criteria (Cavalli-Sforza and Edwards 1967; Farris 1970, 1973, 1978; Kluge and Farris 1969; Felsenstein 1973, 1978, 1979) where objective-ontological usage of parsimony is defended in objective-notational terms. Although variable in detail, numerical parsimony methods are similar in comprising a series of computational procedures designed to minimize biological parameters considered either irrelevant or detrimental to the estimation of true phylogeny. The relevance or weight of particular evolutionary pathways is indicated by a numerical probability derived from a suite of biological inferences. Generally, additive pathways (characterized, for example, by varying degrees of parallelism and convergence) are assigned lower probabilities than more linear patterns. Felsenstein (1978, p. 401) stated, "This class of methods for inferring an evolutionary tree from discrete-character data involves making a reconstruction of the changes in a given set of characters on a given tree, counting the smallest number of times an event need have happened, and using this as the measure of adequacy of the evolutionary tree ... One attempts to find that evolutionary tree that requires the fewest of these evolutionary events to explain the observed data." Given the clearly phenomenological foundation of biological inference and its pivotal role here in determining the credibility of different genealogical arrangements, it is surprising that Cavalli-Sforza and Edwards (1967), Farris (1973, 1978) and Kluge and Farris (1969) implicitly reject ontological parsimony as the basis of their methods. Kluge and Farris (1969, p. 7), for example, state that "Parsimony operates by finding a pattern of relationships that is most consistent with the data. This may not be a 'biological' reason for choosing between alternative trees, but the principle of tailoring theories to fit known facts is an irreplaceable part of science in general." In view of their extraneous nature, the arguments currently advanced by proponents of numerical parsimony criteria will be given no further consideration. In any event, defense of numerical parsimony is hardly enhanced by recognition of its ontological foundation, as the argument then becomes sensitive to the criticisms of Hesse (1974) and Salmon (1961) summarized above.

CONCLUSION

There is no doubt that a thorough re-appraisal of the commitment which phylogenetic systematists have to the principle of parsimony is long overdue. From the preceding discussion it would appear that parsimony is used in an objective-ontological sense in the reconstruction of phylogeny but that this usage is generally camoflaged. It would also seem that apparent objective-notational usage is misleading and that objective-logical usage is misunderstood and potentially unproductive.

It is possible that the time and resources required to produce an unproblematic principle of phylogenetic parsimony will prove to be an investment of diminishing returns. If so, then the last word on the subject should undoubtedly be awarded to Bunge (1961, p. 147), who admonished, "Simplicity is ambiguous as a term and double-edged as a prescription, and it must be controlled by the symptoms of truth rather than be regarded as a factor of truth ... - let us say that a working theory, if simple, works twice as well, but this is trivial. If a practical advice is wanted as a corollary, let this be: Ockham's razor - like all razors - must be handled with care to prevent beheading science in the attempt to shave off some of its pilosities.

FELSENSTEIN, J. 1973. Maximum likelihood and minimum-steps methods for estimating evolutionary trees from data on discrete characters. Syst. Zool. 22: 240-249.
FELSENSTEIN, J. 1978. Cases in which compatibility methods will be positively misleading. Syst. Zool. 27: 401-410.
FELSENSTEIN, J. 1979. Alternative methods of phylogenetic inference and their interrelationship. Syst. Zool. 28: 49-62.
FOSTER, M.H. and M.L. MARTIN (eds.). 1966. Probability confirmation and simplicity. Readings in the philosophy of inductive logic. Odyssey Press Inc., New York.
FRIEDMAN, K.S. 1972. Empirical simplicity as testability. Brit. J. Phil. Sci. 23: 25-33.
GOOD, I.J. 1968. Corroboration, explanation, evolving probability, simplicity and a sharpened razor. Brit. J. Phil. Sci. 19: 123-143.
GOOD, I.J. 1974. A correction concerning complexity. Brit. J. Phil. Sci. 25: 289.
GOODMAN, N. 1943. On the simplicity of ideas. J. Symbolic logic. 8: 107-121.
GOODMAN, N. 1949. The logical simplicity of predicates. J. Symbolic Logic 14: 32-41.
GOODMAN, N. 1950. An improvement in the theory of simplicity. J. Symbolic Logic 14: 228-229.
GOODMAN, N. 1951. The structure of appearance. 3rd ed. D. Reidel Publishing Co., Boston.
GOODMAN, N. 1952. New notes on simplicity. J. Symbolic Logic 17: 189-191.
GOODMAN, N. 1955a. Fact, fiction and forecast. The Bobbs-Merrill Co., Inc., New York.
GOODMAN, N. 1955b. Axiomatic measurement of simplicity. J. Philosophy 52: 709-722.
GOODMAN, N. 1959. Recent developments in the theory of simplicity. Philosophy and Phenomenological Research 19: 429-446.
GOODMAN, N. 1961. Safety, strength, simplicity. Phil. Sci. 28: 150-151.
HARPER, C.W., JR. and N.I. PLATNICK. 1978. Phylogenetic and Cladistic hypotheses: a debate. Syst. Zool. 27: 354-362.
HARRÉ, R. 1972. The philosophies of science. An introductory survey. Oxford University Press, London.
HECHT, M.K. 1976. Phylogenetic inference and methodology as applied to the vertebrate record. In Evolutionary biology, vol. 9. Edited by Hecht, M.K., W.C. Steere and B. Wallace. Plenum Press, New York, pp. 335-363.
HEMPEL, C.G. 1966. Philosophy of natural science. Prentice-Hall Inc., Englewood Cliffs, New Jersey.
HESSE, M. 1974. The structure of scientific inference. The MacMillan Press, Ltd., London.
HILLMAN, D.J. 1962. The measurement of simplicity. Phil. Sci. 29: 225-252.
HOLSINGER, K.E. 1981. Comment: the blunting of Occam's Razor, or to hell with parsimony. Can. J. Zool. 59: 144-146.
INGER, R.F. 1967. The development of a phylogeny of frogs. Evolution 21: 369-384.
JARDINE, N. 1972. A personal report on the fifth annual numerical taxonomy conference, Toronto, November 1971. Syst. Zool. 21: 231-236.
JEFFREYS, H. and D. WRINCH. 1921. On certain fundamental principles of scientific enquiry. Phil. Mag. 42: 369-390.
KAPLAN, A. 1964. The conduct of inquiry. Chandler Publishing Co., San Francisco.
KAPP, R.O. 1958. Ockham's razor and the unification of physical science. Brit. J. Phil. Sci. 8: 265-280.
KEMENY, J.G. 1953. The use of simplicity in induction. Philosophical Review 62: 391-408.
KEMENY, J.G. 1955. Two measures of complexity. J. Phil. 52: 722-733.
KITTS, D.B. 1977. KARL POPPER, verifiability and systematic zoology. Syst. Zool. 26: 185-194.
KITTS, D.B. 1981. Reviews: "Phylogenetic patterns and the evolutionary process: method and theory in comparative biology." Syst. Zool. 30: 94-98.
KLUGE, A.G. and J.S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1-32.
KOHLBERGER, W. 1978. Reviews: "Problems in vertebrate evolution." Syst. Zool. 27: 373-379.

LEQUESNE, J.W. 1964. A method of selection of characters in numerical taxonomy. Syst. Zool. 18: 201-205.
LUNDBERG, J.G. 1973. More on primitiveness, higher level phylogenies and ontogenetic transformations. Syst. Zool. 22: 327-329.
MANDERS, K.L. 1976. Friedman's criterion for simplicity. Brit. J. Phil. Sci. 27: 395-397.
MARSHALL, L.G. 1977. Cladistic analysis of borhyaenoid, dasyuroid, didelphoid and thylacinid (Marsupialia: Mammalia) affinity. Syst. Zool. 26: 410-425.
MICKEVICH, M.F. and M.S. JOHNSON. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Syst. Zool. 25: 260-270.
MITTER, C. 1981. Reviews: "Cladistics and plant systematics: problems and prospects." Syst. Zool. 30: 373-376.
NELSON, G. 1973. The higher level phylogeny of vertebrates. Syst. Zool. 22: 87-91.
NELSON, G. 1978. Ontogeny, phylogeny, paleontology and the biogenetic law. Syst. Zool. 27: 324-345.
PATTERSON, C. 1978. Verifiability in systematics. Syst. Zool. 27: 218-222.
PLATNICK, N.I. 1977a. The hypochiloid spiders: a cladistic analysis, with notes on the Atypoidea (Arachnida, Araneae). Amer. Mus. Nov. 2627: 1-23.
PLATNICK, N.I. 1977b. Cladograms, phylogenetic trees and hypothesis testing. Syst. Zool. 26: 438-442.
PLATNICK, N.I. and G. NELSON. 1978. A method of analysis for historical biogeography. Syst. Zool. 27: 1-16.
POPPER, K.R. 1968a. Conjectures and refutations: the growth of scientific knowledge. Harper Torchbooks, New York.
POPPER, K.R. 1968b. The logic of scientific discovery. Harper Torchbooks, New York.
PRIEST, G. 1976. Discussion: gruesome simplicity. Phil. Sci. 43: 432-437.
QUINE, W.V.O. 1963. On simple theories of a complex world. Synthese 15: 103-106.
QUINE, W.V.O. 1966. The ways of paradox and other essays. Random House, New York.
REICHENBACH, H. 1938. Experience and prediction. An analysis of the foundations and the structure of knowledge. The University of Chicago Press, Chicago.
ROLSTON, H.L. 1976. Discussion: a note on simplicity as a principle for evaluating rival scientific theories. Phil. Sci. 43: 438-440.
ROSEN, D.E. 1974. Phylogeny and zoogeography of salmoniform fishes and relationships of Lepiodgalaxias salamandroides. Amer. Mus. Nat. Hist. Bull. 153: 365-326.
RUDNER, R.S. 1961. An introduction to simplicity. Phil. Sci. 28: 109-119.
SALMON, W.C. 1961. Comments on Barker's "The role of simplicity in explanation." In Current issues in the philosophy of science. Edited by Feigl, H., and G. Maxwell. Holt, Rinehart and Winston, New York, pp. 274-276.
SALMON, W.C. 1973. Logic. 2nd. ed. Prentice-Hall Inc., Englewood Cliffs, New Jersey.
SCHLESINGER, G. 1960a. The principle of minimum assumption. Brit. J. Phil. Sci. 11: 55-59.
SCHLESINGER, G. 1960b. A second note on the principle of minimum assumption. Brit. J. Phil. Sci. 11: 328-329.
SIMON, C.M. 1979. Evolution of periodic cicadas: phylogenetic inferences based on allozymic data. Syst. Zool. 28: 22-39.
SOBER, E. 1975. Simplicity. Clarendon Press, Oxford.
SZALAY, F.S. 1977. Ancestors, descendents, sister groups and testing of phylogenetic hypotheses. Syst. Zool. 26: 12-18.
WILEY, E.O. 1975. Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. Syst. Zool. 24: 233-243.
WILEY. E.O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). Misc. Publ. Univ. Kan. Mus. Nat. Hist. 64: 1-111.