Abstract

Traditional justifications of parsimony in phylogenetic inference assume a correspondence between character-state similarity and steps (character transformation events). In addition to similarity, justifying arguments appeal to conviction, descriptive efficiency, *ad hoc* hypotheses of homoplasy and frequentist probability. Each of these rationales fails in so far as the arguments are incoherent or logically inconsistent with the ontological status of what is assumed and being explained historically. An ideographic justification of parsimony, where character-states constitute transformation events, does, however, allow for a rational preference of most parsimonious phylogenetic hypotheses by invoking the anti-superfluity principle (ASP). According to ASP, explanatory power is maximized by minimizing the number of transformation events required to explain the character-states of the terminal taxa as hypotheses of homology, where the concept homology is restricted to just those *inherited* “things” shared by species. The empirical significance of this rationale is exemplified with the method of direct optimization, which can identify more parsimonious hypotheses than can be confirmed with an analysis of character-state similarities.

A concern for knowledge

A scientific method is valued for its potential to deliver new knowledge. Advances in knowledge are usually founded on the logic of theory-based causal explanation, where hypothesis, \( h \), is sought that has the greatest power to explain evidence, \( e \), in light of background knowledge assumptions, \( b \), and perhaps other auxiliary propositions (e.g., probabilistic models, \( m \)). In practice, a decision making rule/optimality criterion is employed in choosing the preferred \( h \), and it is here that the methodology can be tested for its potential to deliver increased knowledge. The criterion can be evaluated in terms of the operational, how the criterion is measured, or the normative, how the criterion is justified. The purpose of this paper is to examine the coherence and logical consistency of the arguments that have been presumed to justify the parsimony optimality criterion in phylogenetics. In particular, we ask whether or not preference for most parsimonious phylogenetic hypotheses can be justified rationally.

The need for this evaluation of the epistemological underpinnings of phylogenetic parsimony may not be immediately apparent. After all, compared to its rivals, much closer attention has been paid to parsimony’s rational justification, and its sufficiency has been argued from several perspectives. However, as exposed below, several outstanding problems remain to be discussed, and their resolution has substantive empirical consequences in phylogenetic inference. Consider, for example, the three competing explanations shown in Fig. 1 for the five hypothetical equal-length sequences ATGCG, ATGCG, CAGCC, CAAGC and CAAGG. Explanation A requires many more transformation events to explain the variation than the two competitors,
but it requires no homoplasy. As such, according to Farris’s (1983) justification of parsimony, in terms of minimizing ad hoc hypotheses of homoplasy, this explanation is superior to B and equally optimal to C. Alternatively, B and C both require six transformation events, making them equally most parsimonious in that sense, but C could be considered superior to B in that it lacks homoplasy.

We begin by evaluating the arguments that have long been considered sufficient justifications of parsimony in phylogenetic inference, those made by Hennig (1966), Farris (1980, 1983), and Sober (1988). We find that all of these arguments lead to incoherence and/or logical inconsistency, and we then move to a rationale that avoids those kinds of problems. The novel ideographic explication we develop provides an evolutionary epistemology for Wheeler’s (1996) method of direct optimization, which leads to more powerful explanations than those parsimony methods that assume a correspondence between state similarity and steps (Kluge, 2004b, 2005a).

### Traditional justifications of parsimony in phylogenetic inference

Hennig’s (1966, p. 121) “auxiliary principle”, like its subsequent reformulations (e.g., Farris et al., 1970, p. 174, axiom AIII), was intended to provide a sufficient, if not a necessary, argument for identifying homologues in the observations made on organisms, where propositions of homology can then be used as evidence of monophyletic groups of species (Kluge, 2003a). As Hennig (1966, p. 121, brackets in the original) stated,

> ... the presence of apomorphous characters in different species “is always reason for suspecting kinship [i.e., that the species belong to a monophyletic group], and that their origin by convergence should not be assumed a priori” (Hennig, 1953).

As for his justification of this argument (our italics),

This [is] based on the conviction that “phylogenetic systematics would lose all the ground on which it stands” if the presence of apomorphous characters in different species were considered first of all as convergences (or parallelisms), with proof to the contrary required in each case. Rather the burden of proof must be placed on the contention that “in individual cases the progression of common apomorphous characters may be based only on convergence (or parallelism).”

And, it was from this “conviction” that Hennig (1984, p. 51, our translation) was led to a criterion of truth:

The method by which the decision over the assessment of the coherence of features as synapomorphy, convergence or synaplesiomorphy is proven consists then in proving whether they can be brought into harmony with one another. The criterion of truth is consistence.

In an attempt to find an “objective resolution” to the debate between phylogeneticists and pheneticists, Farris (1980) evaluated the different approaches in terms of descriptive efficiency. He found that most parsimonious solutions fully describe the data with the fewest symbols, thus providing a purely operational justification of parsimony.

Nevertheless, Farris (1982; see also Farris, 1967) clarified that descriptive efficiency alone is not a sufficient justification, and he (Farris, 1983) sought to rationalize the preference for most parsimonious solutions in terms of their explanatory power. In doing so, Farris (1983, p. 8) restated Hennig’s auxiliary principle, just as Farris et al. (1970, p. 174) had, i.e.,

> homology should be presumed in the absence of evidence to the contrary.
And, from which he concluded,

This amounts to the precept that homoplasy ought not be postulated beyond necessity, that is to say parsimony.

It was this interpretation that led Farris (1983) to his well-known rationale of parsimony in phylogenetic inference—the minimization of ad hoc hypotheses.

The value of minimizing ad hoc hypotheses is unsailable, as acknowledged by philosophers and scientists alike (e.g., Popper, 1962, p. 288; Wiley, 1981, p. 20; Farris, 1983, p. 18), because such hypotheses are adopted in the absence of any independent rationale, often for the sole purpose of rescuing a preferred hypothesis from refutation. Basically, without such minimization there would be no way of avoiding tautology or of distinguishing personal belief from evidence in choosing among competing theories. Ad hoc hypotheses can also lead to the paradoxical. For example, according to Popper (1957, p. 103), “the ad hoc hypothesis that the laws have changed would ‘explain’ everything”, but in having made such an argument there would be no explanation because the basis for testing is removed.

Farris (1983) was also clear that it was ad hoc hypotheses of a particular kind that are explanatorily superfluous in systematics. As he stated (p. 18; our italics),

the explanatory power of a genealogy is [...] measured by the degree to which it can avoid postulating homoplasies.

And as he amplified later (Farris, 1989, p. 107),

A postulate of homology explains similarities among taxa as inheritance, while one of homoplasy requires that similarities be dismissed as coincidental, so that most parsimonious arrangements have greatest explanatory power.

Lastly, unlike Hennig (1966) and Farris (1980, 1983), Sober (1988, p. 33; see also Farris, 1967; Sober, 1986) took an explicitly probabilistic position on the presence of apomorphous similarities in different species, viewing synapomorphies as providing evidence for monophyletic groups, rather than as absolutely guaranteeing that they must exist. A 110 character does not deductively imply that A and B form a monophyletic group apart from C; nor does a 011 character deductively imply that B and C form a group apart from A. We cannot deduce phylogeny from (polarized) character distributions anymore. Rather, characters are related to phylogenetic hypotheses the way a symptom is often related to a disease. The presence of a symptom may support one disease hypothesis better than it supports another; however, the best-supported hypothesis may be false, even when the symptom is really present. A 110 character favors (A,B)C over A(B,C), because the latter hypothesis would require more changes, and we regard changes as very improbable events. Symmetrically, a 011 character favors A(B,C) over (A,B)C, because the former requires fewer improbable events to explain the observations than the latter. Overall, we prefer that phylogenetic hypothesis that minimizes the number of improbable events it requires. With changes assumed to be very improbable, we are led to a sufficient condition for cladistic parsimony that does not rule out the possibility of incongruent data.

It is this kind of argument that also underlies the use of Bayesian and maximum likelihood methods of analysis in phylogenetic inference (e.g., see Kolaczkowski and Thornton, 2004).

Failures in the traditional justifications of parsimony in phylogenetic inference

We contend that the four justifications of parsimony in phylogenetic inference summarized above cannot be considered sufficient conditions because of the incoherencies and logical inconsistencies identified in their explication. Given that most of these failings have already been discussed in the literature (e.g., see Sober, 1988, pp. 118–121; Kluge, 2003b, 2005a), we only highlight them in the following review.

Conviction

It was Hennig’s (1966, p. 121) “conviction” that, as Farris et al. (1970, p. 174; see also Farris, 1983, p. 8) succinctly stated, “homology should be presumed in the absence of evidence to the contrary.” However, significant problems accompany this exhortation. In particular, Hennig’s conviction does not invoke a logical basis for scientific discovery but is instead a personal opinion that only obtains its normativity by appealing to the consensus of opinion expected from intersubjectivity (Rieppel, 1988, p. 39; 2002). However, intersubjectivity amounts to conventionalism, which does not rationalize the preference because it is not open to objective criticism and does not avoid the claim that science is merely a currently popular belief system indistinguishable from religion or witchcraft (e.g., Feyerabend, 1975). Thus, Hennig’s (1966) “auxiliary principle” is not a sufficient justification of parsimony.

Similarity

There are problems regarding similarity in phylogenetic inference, which calls into question all those arguments for parsimony in which it is critical, as in the “similarity of character-states” (e.g., Hennig, 1966; Farris, 1983; Sober, 1988). To begin with, Darwin’s theory of descent or common ancestry does not require an explanation of similarities among organisms, nor does the concept of homology, although that concept may be used subsequently to explain similarities that are due to inheritance (Farris, 1989, p. 107). As stated succinctly by Hall (1994, p. 7, footnote 4; see also below).
Analogical and homoplasy, not homology, are identified on the basis of similarity of structure or function, similarity being some commonality, not necessarily of the entire features.

Similar character-states may be inherited from the same common ancestral condition, but they do not have to be, as most parsimonious phylogenetic hypotheses repeatedly demonstrate with the discovery of physically identical but independently evolved nucleotide states.

In addition, there is the problem that similarities, by definition, cannot evolve. Similarity is specified in relation to one or more properties, which entails intentional definition. And, that being the case, the properties so defined must be considered immutable, as is the set of organisms that is defined in those terms. Therefore, not only are properties atemporal, the abstract classes they define are not historical individuals, and to treat them as such is reification, i.e., the mental conversion of an abstraction into a thing (Kluge, 2003b). A category mistake is made when the mental concept of a group of similar organisms is reified (e.g., see Rieppel and Kearney, 2002).

Lastly, similarity, and the inductive generalization that accompanies the use of similarities, does not necessarily distinguish a real property from a pseudo-property (Goodman, 1965). Even logically equivalent predicates do not necessarily pick out the same property (Sober, 1982). Basically, there is no guarantee that a predicate can pick out a real (causally efficacious) property in all relevant contexts.

The bottom line is that the concept of similarity is irrelevant to the evolutionary scientist (contra Desutter-Grancolas et al., 2005). Similarity may be useful operationally, but only insofar as it facilitates the ostensive (by reference, pointing, or enumeration) or extensional (denotative) definition of character-states in the delimitation of what are hypothesized transformation series, of which the transformation event(s) are a part (Kluge, 2003b; Grant and Kluge, 2004).

Moreover, one need only take an agnostic position on character-state similarity as evidence of homology to avoid all of these problems (Sober, 1988, p. 119). This can be accomplished with a parsimony analysis of characters defined ideographically, as transformation events (sensu Grant and Kluge, 2004; see also Hennig, 1966, fig. 21), which is capable of discovering monophyletic groups, and with the results of that analysis then being available to test the correspondence between similarity and homology (Farris, 1989, p. 107). In this approach, nothing is assumed that we intend to test and explain (see below).

**Descriptive efficiency**

Description and similarity are interrelated concepts; consequently, many of the criticisms of similarity also apply here. Farris (1982; for the relationship between concepts and operations see also Farris, 1967, pp. 44-45) was the first to highlight the deficiencies of descriptive efficiency as an operationalist justification of parsimony in phylogenetic inference. We add to his list of concerns the fact that descriptive efficiency begs the question of what is to be described efficiently, i.e., what do the symbols represent? Typically, they are described objects in phylogenetics, the states of which are used to formulate diagnoses. It is also the case, as Farris (1980, pp. 390-391) pointed out, that the “same descriptive effect can be achieved by interpreting the diagnoses as a series of evolutionary transformations (that is, as synapomorphies).” However, as we discuss below, diagnostic synapomorphy relations, such as $s_e(A,B)$, are not strictly equivalent to the events qua events of transformation series, $e(A,B)$ (e.g., see Fig. 2; Kluge, 2003b, 2005a,b; Grant and Kluge, 2004).

Elsewhere, we (Grant and Kluge, 2004) argued that the individuation of the observable structure of organisms into character-states and characters (including transformation series, of which transformation events are a part) is a highly theoretical undertaking that cannot be conceptualized in purely descriptive, operational terms. At the very least, it is some set of properties of the perceived objects that are described in terms of similarity relations, not the causal events hypothesized to be responsible for those effects (Kluge, 2003b, 2005a). As Farris (1982, p. 415) underscored, in science that selection is governed by the evidential significance of the observations in achieving causal explanation:

An observation can provide evidence for one theory over another only if it is better explained by one of the alternatives.

However, Popper (1957, p. 77) denied even this much when it comes to description, because

It is not possible for us to observe or to describe a whole piece of the world, or even a whole piece of nature; in fact not even the smallest whole piece may be so described, since all description is necessarily selective.

Although descriptive efficiency may provide a basis for arranging a specified set of symbols or descriptors parsimoniously (Farris, 1980), it fails to justify most parsimonious hypotheses because it does not relate the operational criterion to a real underlying concept of evidence, such as the event in phylogenetic inference, nor to causal explanation. Basically, descriptive efficiency has no epistemological standing in the advancement of scientific knowledge.

A similar argument was made regarding the use of effective complexity, defined as the algorithmic complexity of the regular component of a string of digits, as a measure of information content. As McAllister (2003, p. 306) concluded:
The empirical significance of Wheeler’s (1996) direct optimization method as demonstrated with a hypothetical example taken from Simmons (2004, fig. 1). The evidence consists of five DNA sequences of variable lengths. (A) The optimal alignment obtained \textit{a posteriori} by direct optimization, where the characters are treated as events, \(d_e\), followed by the corresponding most parsimonious network consisting of nine transformation events, \(e(A,B)\). (B) The optimal alignment obtained \textit{a priori}, where the characters are treated as objects and aligned according to similarity, \(d_o\), followed by the corresponding most parsimonious network consisting of 10 transformation events, \(e(A,B)\). See text for further discussion. Other abbreviations: \(M = m\) summed over all transformation series.

The effective complexity of a given string is not uniquely defined. The effective complexity of a string admitting a physical interpretation, such as an empirical data set, depends on the cognitive and practical interests of investigators. The effective complexity of a string regarded as a purely formal construct, lacking a physical interpretation, is either close to zero, or equal to the string’s algorithmic complexity, or arbitrary, depending on which of various possible criteria is used to pick out the regular component of the string.

That is, information, and therefore information content, is context dependent—what is informative in one context may not be in another—and one of the primary roles of discovery operations is to define the domain of informative data (i.e., evidence) for a given class of problems (Grant, 2002). Any discovery operation that fails to do so is incomplete, at best.

**Ad hoc hypotheses of homoplasy**

Homoplasy was central to Farris’s (1983) justification of phylogenetic parsimony—not because of his disdain for homoplasy \textit{per se}, but because he considered homoplasy to be an \textit{ad hoc} hypothesis, and \textit{ad hoc} hypotheses are logically undesirable. “\textit{Ad hoc}” is defined literally as, “For this purpose, to this end; for the particular purpose in hand or in view” (\textit{Oxford English Dictionary}), or “For the particular end or case at hand without consideration of wider application” (\textit{Webster’s Dictionary}). The antonym of \textit{ad hoc}-ness is generality. Thus, an \textit{ad hoc} hypothesis lacks generality; it is put forth to explain a single observation or phenomenon. \textit{Ad hoc} hypotheses are of special concern because one of their most nefarious uses is in rescuing a preferred theory by “explaining away” falsifying observations with a special, unique proposition, and they have been widely discussed by philosophers in that context.

Technically, an \textit{ad hoc} hypothesis is an explanation in which a particular \textit{explanandum} is attributed a unique \textit{explanans}, i.e., an \textit{explanans} that is logically unrelated to other \textit{explananda}, one whose domain includes only that single \textit{explanandum}. Although they are empirical in that they explain empirical observations, and they are not strictly circular or tautological because they do not define the \textit{explanans} as the \textit{explanandum} itself (cf. Popper, 1983, p. 133), their inability to extend beyond the single \textit{explanandum} renders them “almost circular”. Unless rules of inference are devised to protect a system of knowledge from \textit{ad hoc} hypotheses, every observation could be explained by its own, special theory, rendering that system of knowledge empirically empty. As such, hypothesis optimality is inversely related to degree of \textit{ad hoc}-ness.

The problem we identify in Farris’s (1983) rationale is not its focus on \textit{ad hoc}-ness, but rather the premise that a statement of homoplasy entails an \textit{ad hoc} hypothesis. Homoplasy cannot be an \textit{ad hoc} hypothesis because it is not a hypothesis; it is an acausal description, not a causal explanation (Kluge, 1999). Explanation is attributed to each of the underlying transformation events, which are merely described as homoplasious. Furthermore, when propositions of homology are tested with character congruence, and from which homoplasy is inferred (\textit{sensu} Farris, 1983), homology and homoplasy become a complementary relation, a and not-a, respectively (see however, Fitch, 2004). As the not-a relation, Kluge (1999, p. 434) concluded that “homoplasy is an abstraction and may be understood only nominally, e.g., as some minimal amount of error in the inference of homology.” However, there can be no
natural causal explanation for such error. Although homoplasy as systematic error may be defined intentionally as a class concept, it cannot be modeled as if it were a historical law. Of course, increasing precision by minimizing error is a worthwhile endeavor in all sciences, but it has no epistemological standing itself. As Popper (1979, pp. 356–357) recognized, a “precise statement can be more easily refuted than a vague one, and can therefore be better tested.” However, as he went on to note, the theoretical or the explanatory has logical priority over the practical or “instrumental” tasks of science, like those of precision.

Still further, homoplasy is defined conceptually in terms of similarity, yet similarity per se is irrelevant to phylogenetic inference (see above). Specifically, homoplasy refers to similarities in structure, development, or function that are due to transformation events in different lineages. By definition, those objects are causally independent of each other, so there can be no common evolutionary, phylogenetic explanation of homoplasy. Aside from the criticisms that have been lodged against using similarity in the inference of phylogeny (Hennig, 1966; Farris et al., 1970; Kluge, 2003b, 2005a), homoplasy cannot be explained in evolutionary terms when it is defined intentionally as an immutable set of similarity relations. Only ostensively defined, spatio-temporally restricted particulars have the potential to evolve according to Darwin’s theory of “descent, with modification” (contra Sander-son and Hufford, 1996). Insofar as they may be phylogenetically relevant, so called “explanations” of homoplasy (e.g., neoteny) result in the exclusion of certain observations from consideration as independent transformation series (i.e., the claim that they are not separately evidentially significant, whereby a single transformation event is invoked to account for multiple variants). Nothing in these criticisms of homoplasy denies natural selection as a valid explanation generally; it is denied only when it is incorrectly applied to a set of independently evolved (and therefore causally independent) yet similar things (for further discussion see Kluge, 2005b). Adaptationist or selectionist “explanations” of homoplasy require the prior reification of homoplasy for their validity. From an evolutionary perspective, what is actually in need of adaptationist explanation is not the set of similar objects that evolved in different lineages, but each particular thing in each particular lineage, i.e., those things that are historically necessarily unique (Kluge, 2003b, 2005a,b). Having discovered that similar things evolved independently may provide a heuristic guide in the formulation and testing of adaptationist hypotheses at the level of populations, but that plays no role in the adaptationist explanation itself (Kluge, 2005b). If nature has taught us anything, it would be that living things respond to the same selective pressures in any number of ways, a lesson that is anathema to inductive reasoning in adaptationist, comparative biology (Kluge, 2005b).

The ideographic nature of phylogenetic inference itself provides another argument against the explanatory relevance of homoplasy. As Grant and Kluge (2004) observed, it is the ostensively defined transformation series that is significant in choosing the hypothesis that maximizes explanatory power. We believe this is the same interpretation Hennig (1966, p. 90) attributed to autapomorphous characters. As he stated,

apomorphous features characteristic for a particular monophyletic group (present only in it) can be ignored in discussing its relations to other groups; we will call such characters the autapomorphic characters of a monophyletic group.

The critical point in this argument is that all apomorphies originate as autapomorphies through lineage-specific transformation events, and they are only rendered homoplasious and synapomorphic by independent events—homoplasious by independent transformation events in different lineages and synapomorphic by subsequent cladogenetic events in the same lineage. Thus, whether emphasis is placed on individuating the event or the object, it is the historically unique character-state that identifies a particular monophyletic group.

Lastly, Sober (1988, pp. 135–141) reiterated the long-standing criticism that minimizing an ad hoc hypothesis of homoplasy assumes that homoplasies are rare. And, as he went on to argue, a problem remains even if it were possible to determine the assumptions of the method by looking at what optimal hypotheses assert (e.g., see Farris, 1983, pp. 13–14; see also below). As Sober (p. 141) concluded:

Parsimonious hypotheses place lower bounds on the number of homoplasies that are less constraining than the lower bounds imposed by their less parsimonious competitors. In this respect, they minimize assumptions without assuming minimality. But how this translates into an overall assessment of the phylogenetic hypotheses themselves remains to be seen.

Frequentist probability

Sober’s (1986, 1988) justification of parsimony assumes a frequentist interpretation of the evidence, which is antithetical to an ideographic science like phylogenetic systematics. Given that the monophyletic parts of phylogeny are necessarily unique (Kluge, 2002), as is the character evidence used in the inference of such things (Kluge, 2003b), whatever position is taken in discussions of epistemology it must be consistent with that ontology. Whether hypotheses are selected through explicitly statistical (e.g., maximum likelihood) or non-statistical (e.g., weighted parsimony) means, the implementation of the frequentist methods and principles of
nomothetic disciplines in ideographic science leads to logical inconsistencies that compromise the validity of all resulting empirical inferences (Grant, 2002).

**ASP, an ideographic justification of parsimony in phylogenetic inference**

There remains the possibility of identifying a justification of parsimony that avoids the aforementioned problems, and the evolutionary assumptions of which amount to no more than “descent, with modification”, **b**. We believe this is possible with the synthesis of three publications. First, Farris (1967) divided evolutionary relationship into cladistic and patristic relationships, thus defining conceptually the problem of phylogenetic inference. That is, phylogenetic hypotheses, **h**, are composite explanations consisting of hypotheses of monophyly (cladogenetic events, topology) and homology (character transformation events, historical identity relations).

Second, Baker (2003), building primarily on the work of Barnes (2000; see also Davidson, 1991), identified a particular kind of anti-superfluity principle (ASP) according to which explanatory power is maximized by minimizing the explanatorily equivalent causal entities that must be postulated to account for some phenomenon. Baker’s ASP pertains only to explanations that are demonstrably additive. As he clarified (p. 248),

> The explanation is “additive” in the sense that the overall phenomenon is explained by totaling the individual positive contributions of each object [or event].

In such cases, “quantitative parsimony tends to increase the explanatory power of hypotheses compared to their less quantitatively parsimonious rivals” (p. 248). A less quantitatively parsimonious hypothesis can only match the most quantitatively parsimonious proposition in explanatory power by adding auxiliary claims. “Thus the preference for quantitatively parsimonious hypotheses emerges as one facet of a more general preference for hypotheses with greater explanatory power” (p. 258). (For further details see Kluge, 2005a).

Finally, Grant and Kluge’s (2004) ideographic concept of character linked the contributions of Farris and Baker by identifying inferred transformation events as the evidentiary entities of phylogenetic explanation. Under this concept of character, each inferred transformation event is explanatorily equivalent, and the explanation of the character-states observed in terminal taxa is achieved by summing the postulated events over the entire phylogeny, thus satisfying Baker’s (2003) ASP requirement of additivity.

The virtue of minimizing the quantitatively superfluous in phylogenetic inference—the patristic distance—is that collectively the inferred transformation events (Hennig, 1966, fig. 21; not synapomorphic similarity, pp. 93–95) account directly for character-states as nested series of homology relations. The explanation is “additive” in the sense that the individual positive contributions of each transformation event are summed, and explanatory power increases to the extent that they are minimized by the phylogenetic hypothesis. Preference for less quantitatively parsimonious hypotheses can only be justified by adding auxiliary claims of one sort or another, which are themselves explanatorily superfluous, and therefore further decrease their explanatory power relative to their more parsimonious rivals.

Furthermore, by relating the transformation events to each other and to cladogenetic events (and vice versa), the explanations that emerge from phylogenetic analysis reach beyond the premises of the analysis and deliver genuine knowledge claims. These not only include the relationship between similarity and inheritance, but even its basis in DNA (e.g., Doucet et al., 2004; see however, Driskell et al., 2002).

We call the reader’s attention to the fact that our ideographic explication does not involve dissimilarity comparisons. Setting aside similarity means more than discounting raw (overall) similarity, which conflates symplesiomorphy, synapomorphy and autapomorphy (Hennig, 1966; Kluge, 2003b). It also means setting aside the concept of special (synapomorphic) similarity, s(A,B), i.e., similar shared-derived character-states between taxa A and B. At most, in conceptual terms, one might say that phylogenetic systematics is left with a kind of similarity “owing to ancestral states”, sE(A,B) (Farris et al., 1970, p. 187; see also Farris, 1967; see however, below). In distinguishing between s(A,B) and sE(A,B), Farris et al. (1970, p. 187) pointed out:

> The actual choice of a phyletic tree is left to an algorithm that effectively constructs the evolutionary hypothesis most in accord with available data. Thus only a weak connection between s or sE and relationship is assumed.

For example, the Wagner parsimony algorithm remains a useful tool for identifying most parsimonious hypotheses with classically defined character-state data (Kluge and Farris, 1969; Farris, 1970). However, steps (transformation events) do not necessarily correspond to similar states. As Farris (1967) pointed out, patristic and phenetic differences are not the same. As he illustrated in his fig. 1, in what some mistakenly consider a trivial example, there are homoplaxious character-states that are irreducibly similar. In addition, transformation events must be considered historically independent of each other, because they are spatio-temporally independent entities (Grant and Kluge, 2004). Similar character-states cannot be so considered (e.g., see Simmons, 2004, fig. 1). In spite of having made the conceptual distinction between steps
and similarities, post-Hennigian cladistics drifted towards a concern for perceived patterns, and with it the systematic character was used in purely operational terms, as character-state similarity relations (Kluge and Farris, 1999; Kluge, 2003b, 2005a; Grant and Kluge, 2004).

Grant and Kluge’s (2004) ideographic definition of character opposed that trend; theirs was an event concept, events being things that happen, such as character-state transformations and cladogenesis. That definition is not an object concept—objects being things to which physical features are attributed, like volume, mass and being containable and storable—even though the object is the thing that systematists observe when operationalizing the concept character and geneticists currently use in their measurement of heritability, i.e., the proportion of the variance in a trait among individuals that is attributable to differences in genotype. What is it, then, that allowed Grant and Kluge to argue that their transformation series character concept is concerned with inheritance when the ontological distinctions between event and object imply their incommensurability? To begin with, the problem is simplified by virtue of the fact that the transformation event(s) and the transformed object(s) form a spatio-temporally restricted, historically contingent, transformation series (Hennig, 1966). That is, the locatability and mobility of the event are not a problem with reference to the object—they are causally related, and consequently, paraphrasing Woodger (1929, pp. 301–302), it can be stated that the physical object, which we call the character-state, is expressive of certain of the knowable characteristics of the event that can be exemplified in sense-experience. That is, for the purposes of phylogenetic inference, the character-state is the event and the event is the character-state, or, in a word, the event and object are causally coextensive. Thus, for example, the ontological distinctness of mutation (event) and mutant (object) concepts does not deny their causal continuity and their comparability in terms such as inheritance. The concept of character transformation most certainly does not involve an ontological mistake, a category error (contra Hay and Mabberley, 1994; Sattler, 1994). Indeed, it is because transformation events are phenomenologically the same in the causal law of inheritance that they are considered identical and additive (Davidson, 1991; Baker, 2003).

With regard to the systematists’ and geneticists’ character discovery operations, it is important to recognize that the phenotypic states that are attributed to an organism are, at best, only proxies for the actual “stages of expression” in a transformation series (Hennig, 1966, p. 91). For example, no one should believe that the states of eye color and handedness in humans are passed literally from parent to offspring or are the material objects that undergo heritable transformation. None of this denies the evidential significance of phenotypic data. However, it does suggest that progress may be achieved in future research cycles by honing in on the genetic bases that underlie transformation events inferred from variations in the phenotype. For example, given an initial amino acid sequence, one may further test and refine phylogenetic explanations by discovering the transformation events in the underlying DNA sequence, thereby eliminating error due to the redundancy of the genetic code.

ASP and the meagerness of assumptions

As Sober (1986, p. 41, 1988) declared

I have suggested a [likelihood] framework, which, if true, suffices to justify parsimony.

But, he also had to admit:

The possibility always remains that different or more meager assumptions will suffice to legitimize the method.

Like all statistical approaches to phylogenetic inference, Sober’s (1988) likelihood justification requires an evolutionary model, the parameters of which involve propositions in addition to the assumptions of Darwin’s “descent, with modification” as background knowledge, b (Sober, 2004). Likewise, weighted-parsimony methods also require assumptions about the probability or importance of classes of changes, in addition to b. In addition to these model assumptions being counterfactual, according to our explication, all such assumptions beyond b are unnecessary for achieving phylogenetic explanation, rendering them explanatorily superfluous, i.e., more meager assumptions suffice to legitimize the method: “descent, with modification”, b, provides the causal basis sufficient to infer transformation events as historical identity relations, those of monophyly and

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1Event and process are related conceptually but are not synonymous. The most salient difference is that events are temporally bounded, whereas processes are unbounded. That is, the distinction hinges on perspective and scale. For example, the process of evolution is open and ongoing, whereas the particular event of the evolutionary origin of bird wings is closed. Because both are temporal concepts, common language often fails to distinguish between them, and intended meaning is contextual.

2A counterfactual is a conditional argument of the form “if p were to happen q would”, or “if p were true q would be true”, where the supposition of p is contrary to the known fact not-p (Lewis, 1973). For instance, the “common mechanism” models assumed in most maximum likelihood models are counterfactual because transformation events are causally independent, i.e., “no common mechanism” is the general case. Counterfactuals are a powerful philosophical tool to expose logical fallacies, but their application in empirical inference is problematic. (For further discussion, see Grant, 2002.)
homology in turn, and ASP is sufficient for justifying the minimization of those entities as maximizing explanatory power in unweighted parsimony.

Detractors may counter that parsimony (including our explication) differs from statistical, model-based methods only in that its probabilistic assumptions are implicit. Indeed, many workers have followed Felsenstein (1978) in attempting to elucidate those implicit probabilistic assumptions, and it is the severity of those putative assumptions that is often cited as the basis for preferring methods other than parsimony. However, the search for implicit probabilistic assumptions itself relies on the assumption that methods can only be understood in purely statistical, probabilistic terms. In response, it is instructive to consider the implications of finding that the most parsimonious tree is the maximum likelihood solution may be achieved without recourse to those additional, and therefore superfluous, assumptions.

**ASP and explanatory power restated**

According to Popper (1962, p. 58; italics in original), as scientists we do not seek highly probable theories but explanations; that is to say, powerful and improbable theories. Thus, we are led to Popper’s formalism, $E(h, e, b)$, which is the power of hypothesis, $h$, to explain evidence, $e$, given background knowledge, $b$ (Popper, 1959, p. 401; Salmon, 1966, p. 46). The origin and justification of this kind of explanation are straightforward, because $E(h, e, b)$ is derived from precisely the same terms as Popper’s severity of test, $S(e, h, b) = p(e, h) - p(e, b)/p(e, b) + p(e, b)$, which defines the support of $h$ by $e$, in the presence of $b$ (for a summary see Kluge, 1997, 2001, 2003a). Thus, explanatory power, like severity of test, has nothing to do with a statistical assessment of when sufficient data have been acquired; Popper’s explanatory power is maximized deductively, not inductively (contra de Queiroz and Poe, 2001, 2003; de Queiroz, 2004). Popper’s explanatory power and ASP are related naturally by the fact that a theory that postulates fewer entities prohibits more and is therefore less probable, more testable, and of greater explanatory power than one that postulates more such entities.

Darwin’s first two principles of evolution, “descent, with modification”, constitute sufficient background knowledge, $b$, to justify monophyletic groups, $D_e$, and transformation series, $d_e$, in the inference of phylogeny, in so far as they equate to Farris’ (1967) evolutionary components of cladistic and patristic relationships, respectively. In addition to “descent, with modification”, Darwin (1859, pp. 111–126) also included the principles of natural selection and extinction in his arguments for the distinctiveness of groups of taxa and character divergence. While “descent, with modification”, may be considered lawful parts of a deductive explanans (Kluge, 2003a), natural selection and extinction cannot be. Consider, for example, that the processes of selective neutrality and meiotic drive are known to be responsible for some character evolution, and which can be of a divergent nature. Furthermore, while the vast majority of species lineages have no doubt become extinct, the presence of at least a relatively few extant species shows that even lineage extinction cannot be construed as a universal condition. Thus, natural selection and extinction can only be referenced as non-lawful conditions in an inductive explanans—as modeled assertions, $m$, about particular facts—bearing in mind that it is the explanans that makes the explanandum.

Species are taken to be the spatio-temporally restricted parts of a lineage system—a parent species transforming into sister species—just as characters are considered to be the individually heritable and transforming parts of that system (Hennig, 1966; Grant and Kluge, 2004). Explanation is achieved by causally relating the character-states observed in multiple species through their shared transformation events. That is, characters (transformation series) are determined by the inferred transformation events required to explain the character-states observed in the terminal taxa. In general terms, the greater the asymmetry between the number of entities to be explained and the number of entities postulated to explain them, the more powerful the explanation. Consequently, the fewer the transformation events required to explain the character-states of terminal taxa, the greater the explanatory power.

More technically, the explananda, $e$, are the character-states (sensu Grant and Kluge, 2004) of terminal taxa, which are explained by postulating a particular hypothesis of phylogenetic relationships (i.e., a hypothesis of cladistic and patristic relationships; Farris, 1967), $h$, in light of the background knowledge of “descent, with modification”, $b$. Together, $b$ and $h$ constitute the explanans. The number of possible hypotheses of evolutionary relationships, $h$, is given by pure logic and can be enumerated as a function of the number of terminals (Siddall and Kluge, 1997; Grant and Kluge,
2004) and, assuming ASP as a necessary prior philosophical assumption, the number of character-states, \( e \), identified for terminal taxa (cf. Wheeler, 1996). Choice among hypotheses, \( h_1, h_2, h_3, \ldots, h_n \), is made on the basis of their explanatory power: the \( h \) that which minimizes the number of transformation events hypothesized to explain the character-states of terminal taxa as homologues is optimal.

A phylogenetic analysis, the testing of \( h \) with \( e \), is justified because the history of characters is coextensive with the history of species (Grant and Kluge, 2004). Severity of test is maximized by evaluating the ability of competing hypotheses, \( h_1, h_2, h_3, \ldots, h_n \), to explain all \( e \) simultaneously, not subsets of \( e \) (Kluge, 2004a). Moreover, as already noted above, phylogenetic hypotheses are composite explanations: hypotheses of monophyly (cladogenetic events, topology) and homology (character transformation events, historical identity relations). Traditionally, in phylogenetic systematics, explanation has been explained in terms of the cladogram, \( D_e \), with emphasis placed on choosing among competing cladistic hypotheses. Thus, the hypothesis of cladistic relationships that allows the minimization of the overall patristic distance is the objectively optimal phylogenetic theory, because it has the greatest power to explain the character-states of terminal taxa as nested hypotheses of homology. Alternatively, emphasis may be placed on choosing among competing patristic hypotheses: as justified by ASP, transformation events are minimized because fewer hypotheses are required to explain the evidence, \( e \), as propositions of homology, \( d_e \). We prefer the latter emphasis, because that is where the parsimony basis for hypothesis choice lies. This can be restated simply as: explanatory power is maximized by minimizing the number of transformation events required to explain the character-states of the terminal taxa as hypotheses of homology. In any case, to allow for a more complex history of character evolution is to protect the system from being falsified (Popper, 1959, p. 145).

According to Lakatos (1993, p. 116; our italics; see also Kluge, 1997), testability must be “sophisticated”, in the sense that there is interplay between evidence, \( e \), and competing hypotheses, \( h_1, h_2, h_3, \ldots, h_n \), that “leads to the discovery of novel facts.” Such a progressive problem shift indicates a situation in which hypothesis \( h_1 \) suggests something more than hypothesis \( h_2 \) suggested, as well as suggesting more than is required by the data themselves. Knowledge of such a novel nature can be obtained from tests suggested by the most parsimonious cladogram, \( D_e \), independent of the test of character congruence. That knowledge can come from phylogenetic inference being practiced as a reciprocally illuminating kind of science (Hennig, 1966; Kluge, 1998, 1999).

### The empirical significance of ASP in phylogenetic inference

Evolutionary, \( e \), and phenetic, \( p \), approaches to phylogenetic inference are epistemologically opposed: the former seeks to explain biological variation, the latter aims to describe it. Moreover, far from being a preoccupation only of modern biologists, or even a consequence of Darwinian theorizing, this distinction has been at the heart of systematics since its origin as a science (Sloan, 1979; contra Brady, 1985). As Kant summarized in 1775 (translation from Sloan, 1992),

> The logical division [of Linnaeus] proceeds by classes according to similarities; the natural division considers them according to the stem [Stämme], and divides animals according to genealogy, and with reference to reproduction. One produces an arbitrary system for the memory, the other a natural system for the understanding [Verstand]. The first has only the intention of bringing creation under titles; the second intends to bring it under laws.

Involved in this difference is the distinction between the event, i.e., character transformations and cladogenesis, and the object, i.e., the physical things that scientists claim to “observe” (Kluge, 2003b). In the event-based approach to phylogenetic inference, explanatory power is maximized by the phylogenetic hypothesis, \( h \), that requires the fewest transformation events (minimum patristic distance) to explain the character-state data, \( d_e \). As such, no special epistemological or empirical importance is attributed to data matrices; they are simply representations of character-states aligned into transformation series, i.e., a summary of homologues, and causal explanation obtains from the character-state transformation events being optimized on the cladogram as hypotheses of homology.

An alternative position holds that data matrices are epistemologically and empirically relevant, that they contribute to the explanation of observed biological diversity. According to this position, features are first arranged in a matrix according to similarity, and these similarity statements constitute a basis for describing biological variation, \( d_p \) (Kluge, 2003b). A branching pattern, \( D_p \), is sought which allows the most efficient description of the special (synapomorphy) or raw (overall) similarities, \( d_p \), in the character matrix (Farris, 1980). As noted above, explanation may be claimed subsequently by identifying the hypotheses of homology that are consistent with that descriptively optimal arrangement, but the analytical emphasis is placed on acausal description, not causal explanation. This is

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3Although direct observation is often contrasted with indirect inference, these are at best points on a continuum, and all empirical claims are hypothetical, regardless of whether they relate to objects or events.
the major problem with descriptive efficiency as a parsimony rationale in phylogenetic inference (Farris, 1982). That most efficiently described objects might be explained subsequently as homologous, homoplasious and autapomorphic does not necessarily mean objects and events have the same epistemological standing.

Maximizing the explanatory power and descriptive efficiency of a given data matrix can result in the same most parsimonious hypothesis of species relationships, as in the analysis of fixed (static) matrices (Farris, 1982). However, that finding does not hold generally. The quantitative ASP justification of parsimony outlined above is empirically relevant in that it offers a basis for hypothesis choice. For example, the competing explanations shown in Fig. 1B and C are equally optimal, despite their differing levels of homoplasy, and both are superior to A in maximizing explanatory power.

Moreover, ASP provides an evolutionary epistemological justification for Wheeler’s (1996) direct optimization approach to phylogenetic analysis of DNA sequences (see also Sankoff, 1975; Sankoff et al., 1976; Wheeler, 1994; Carpenter, 2003). Although the computational complexity of the problem requires numerous heuristics, the logic behind this approach is that all possible evolutionary hypotheses (i.e., cladistic and patristic relationships) may be evaluated in searching for the explanation that requires the fewest character transformation events, that being the hypothesis of greatest explanatory power (sensu ASP). Other methods that claim parsimony as their optimality criterion (Simmons, 2004; see also Zurawski and Clegg, 1987; Golenberg et al., 1993) are phenetic in that they apply that criterion to the matrix where the characters are treated as objects (having similar properties), $d_p$, not to the transformation series, $d_e$, where the characters are treated as events (transformations), and in doing so may choose solutions of less explanatory power. The effect of this distinction is illustrated in Fig. 2, where a more parsimonious hypothesis is obtained from direct optimization (Fig. 2A), i.e., the optimization of characters as transformation series on a topology, than can be discovered from an analysis of a similarity matrix of nucleotide states (Fig. 2B).

Conclusions

Only non-evolutionary description is possible when $d_p$ and $D_p$ are employed. However, many phylogeneticists continue to assert that similarity underlies all evidentiary and taxonomic relations, $d_p$ and $D_p$ and $s(A,B)$, respectively (e.g., Desutter-Grandcolas et al., 2005). To the contrary, our findings lead us to conclude, in stressing coherence and logical consistency, that it is the transformation event, $e$, and not the similarity of the object, $p$, which underlies those relations. In a historical science like phylogenetic systematics, it is $d_e$ and $D_e$ that provide the basis for explanatory power. Even similarity owing to ancestral states, $s_E(A,B)$, is not necessarily the same as $e(A,B)$ (see Fig. 2). With these distinctions in mind, phylogeneticists may be guided towards a scientifically rigorous, coherent and logically consistent form of causal explanation. Summarizing, $d_p$ and $D_p$ ≠ $d_e$ and $D_e$, and $s(A,B)$ and $s_E(A,B)$ ≠ $e(A,B)$. It is our position that only $d_e$ and $D_e$ and $e(A,B)$ offer evolutionary explanation and real advances in empirical knowledge.

Advances in theory also follow from this world-view. For example, the concept homology becomes exclusively evolutionary when character and character-state are treated ideographically. In this context, homology is restricted to just those inherited “things” shared by species (Kluge, 2003a, 2003b). Whereas, the traditional, more inclusive, meaning of homology is “anything” derived from a common ancestor, such as similarity relations, but which do not necessarily have a basis in evolutionary theory.

References


